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1

A New Dwarf Toad from Southeastern Brazil

George S. Myers & Antenor Leitão de Carvalho

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THE authors have examined a large series of the comon South American toad, *Bufo granulosus* Spix (called also *B. globulosus* Spix), from the lower Amazon (Manaus, Santarém), the Rio Araguaya, Ceará, Minas Gerais, and the upper Rio Paraguay (São Luiz de Cáceres). These show clearly that this widespread species varies geographically with considerable consistency, and that several subspecies will probably be recognized eventually.

The large series from the Araguaya (Rio Tapirapé) shows a flattened muzzle which easily separates this lot from the toads we collected at Pirapora in Minas Gerais, and, indeed, from the Manaus and Santarém examples. The São Luis de Cáceres individual exhibits a peculiar shortened physiognomy and strong infranarial crest different from all the others. In some ways this specimen approaches two toads from Asunción, Paraguay, which we were at first inclined to call *Bufo d'orbignyi* Duméril & Bibron. However, we have not seen typical examples of the latter (from Uruguay) and Boulenger's 1882 figure of the head of *B. d'orbignyi* (Montevideo specimen), which shows no serrations or warts on the cranial crests, leads us to suspect that these Asunción toads may lend weight to Parker's (1936) suggestion that the flat-headed *B. granulosus* and the deep-headed *B. d'orbignyi* intergrade in the Paraguay Basin.

Strikingly different from all the toads of this type that we have examined is a fine series collected by the junior author in the *restinga* (scrub beach vegetation) of the eastern part of the State of Rio de Janeiro. These represent a form close to typical *B. granulosus* but sharply distinct in its minute size, striking coloration and different cranial morphology. While there is a possibility that this strange little toad (perhaps the smallest South American *Bufo*) will eventually be found to intergrade with *B. granulosus*, we are not sure of this, and, on the basis of our material, venture to predict the existence, in the littoral district of the State of Rio and perhaps a wider area, of a quite distinct, pigmy species of *Bufo* belonging to the *granulosus* complex and agreeing fairly well with the following diagnosis.

Bufo pygmaeus, new species

Holotype.—An adult male of average size, 37.5 mm. in snout-to-vent measurement, taken while calling by A. L. de Carvalho and L. de Castro Faria at Saõ João da Barra, at the mouth of the Rio Parahyba (right bank), State of Rio de Janeiro, Brazil, in December, 1948. To be deposited in the Museu Nacional, Rio de Janeiro.

Paratypes.—Eighty-five examples, taken with the holotype while in breeding congress, and at the same time and place. Most of the paratypes are in the Museu Nacional, Rio de Janeiro. Others are in the Natural History Museum of Stanford University (nos. 10720-10723). Two have been sent to the U. S. National Museum. The specimens are all adult, even the smallest males possessing a vocal sac and a nuptial pad on the first finger of each hand.

Other material.—Three examples in the Museu Nacional from the Restinga de Marambaia, to the westward of the city of Rio de Janeiro, indicating a general distribution in the littoral region of the State of Rio de Janeiro.

Diagnosis.—Similar in most respects to *Bufo granulosus* Spix but differing especially in the very small size (largest female 42 mm. in head and body length; largest male 41 mm.); in the much bolder light-and-dark mottling and marbling of the dorsum; in the much stronger development of a longer, curved, supratympanal crest; in the unserrated subocular crest; and, above all, in the development of a strong parietal crest.

Discussion.—This small toad is a vicarious (allopatric) form of the *granulosus* complex but, insofar as our material shows, it is a distinct species. In *B. granulosus*, most of the bony crests

TABLE 1. MEASUREMENTS OF *Bufo pygmaeus* IN MILLIMETERS

Specimens[1]	1♂	2♂	3♂	4♀	5♂	6♂	7♂	8♂	9♂	10♂	11♂	12♂	13♂	14♂	15♂	16♂	17♂	18♂	19♂	20♀	21♀
Total length, head and body	39	38	34	34	36	36	35	41	35.6	38.5	37.5	34	36	30	34	29	27.5	25	25	31	42
Length of femur	12	12	10.5	10	10.8	11	10.2	12.2	11.5	12	11	10	11	9	10	9	8	8	7.5	9	12.5
Length of tibia	11.5	11.2	10	9	9.8	10	9.5	11.2	10	11.2	11	9.8	10.5	8	9.5	8.8	7.2	7.1	7.5	8.5	12
Length of foot incl. tarsus	18	18.5	16.5	15	16	17.5	15	21	17	17	18	16	17	13	16.5	14	12	12	12	14.5	18.8
Width of head	13	13	11	11.6	12.5	12.5	11.5	14	12.5	13.2	13	12.2	12.5	10.5	12	10.5	9.5	9.5	9.5	11	15

[1] Specimens 1-4 in Stanford. Specimen No. 11 is the holotype.

of the head are strongly serrated or warty. This tendency is sharply reduced in *B. pygmaeus,* the almost straight, almost invariably unserrated suborbital, labial and postorbital crests being especially notable. In *B. granulosus* the supratympanal ridge is short, broken, and composed of one or two rows of warts or short ridges. In *B. pygmaeus* this crest is longer, sharper, less broken, and usually consists of one strong ridge, sharply incurved at its posterior end. The parietal crest is often indicated in *B. granulosus* by a collection of two or three warts behind the posterior curve of the supraorbital crest. There is almost never more than this in any material seen by us except a single strange example from São Luis de Cáceres, on the upper Rio Paraguay in Mato Grosso, which appears to show an approach to *B. d'orbignyi* but which is vastly different from *B. pygmaeus* in many characters besides its sharp and overly developed subnarial crest. The posterior curve of the supraorbital crest in *B. granulosus* is typically formed of a series of small parallel bony folds or ridges and in an occasional example one of these is weakly continued towards the parietal region by a broken ridge. In *B. pygmaeus,* on the other hand, these supraorbital folds are much coarser and better developed (usually about four in number) and one of them (first, second, or third) is produced inward as a very strong parietal crest.

The two Paraguayan toads mentioned in our introduction have the folds of the supraorbital crest much more strongly developed and still fewer in number. In fact, these cranial characters lead us to suspect that the *B. granulosus* complex may ultimately be considered a *Rassenkreis,* the northerly forms now called *granulosus* intergrading with *d'orbignyi* in the Paraguay Basin, and the latter perhaps intergrading with *pygmaeus* northward along the coast towards Rio de Janeiro.

Note on Bufo nasicus *Werner.*—In connection with our search through the literature we have considered the recent paper by Smith & Laurent (1950, Inst. Royal Sci. Nat. Belgique, Bull., tome 26, no. 21, 3 pp.) on the type of *Bufo nasicus* Werner, which, on the basis of insects identified from the stomach contents of the type, those authors believe must have come from eastern South America. *B. nasicus* bears no close relationship to *B. pygmaeus.* After comparison of the description and figures of Werner's type with a specimen of almost exactly the same size, we suggest that *B. nasicus* was based on an example of one of the several races of *B. typhonius,* probably from southeastern Brazil.

Note on the names Bufo globulosus *Spix and* B. granulosus *Spix.*—Spix (1824, Spec. Nov. Test. Ran.) described two new toads, *Bufo*

globulosus and *B. granulosus,* in the same paper. Peters (1872, Mb. Akad. Wiss. Berlin, pp. 223, 226) re-examined the types of both and definitely synonymized the names. Peters selected the trivial name *granulosus* instead of *globulosus,* and the species has been called *Bufo granulosus* by almost all authors. Peters's act in selecting *granulosus* over *globulosus,* although the latter name has page priority, is sanctioned by Article 28 of the International Rules of Zoological Nomenclature. However, in what we consider to be an ill-advised repeal of this basic "rule of the first reviser," the recent International Zoological Congress at Paris has made it mandatory to accept page priority as the basis for selecting names of this type, although with a provision that cases in which confusion will be caused may be brought before the International Commission on Zoological Nomenclature for decision. *Bufo granulosus* is one of the commonest toads in South America, and we see no reason to change its name because the International Congress chose to make a basic change in the International Rules, a change that will cause a great deal of confusion.

In regard to the zoological question of the specific identity of the types of Spix's two names, Peters's decision has not been questioned, nor can we see that his decision can be assailed, for the types are no longer in existence. Nevertheless, we have compared *B. pygmaeus* carefully with Spix's descriptions and figures and do not believe that either of his names was based on *B. pygmaeus.*

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2

Sexual Broods and the Production of Young Queens in Two Species of Army Ants[1]

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(Plates I-III; Text-figures 1 & 2)

HOW species of doryline ants produce their males and young queens is a biological enigma of long standing, toward the solution of which this paper is directed. The processes of sexual-brood production in these ants also prove to be important as prerequisites to colony division, a problem which will be considered in a further paper.

The problems of caste control and sex dimorphism have recently grown in interest for biologists (Flanders, 1939, 1950; Haydak, 1943; Whiting, 1943, 1945; Kerr, 1946; Berland, 1948). Although progress has been made, the basic processes are not well understood. The Dzierzon rule for insects, according to which males develop from unfertilized eggs and females from fertilized eggs (Newall, 1915; Wigglesworth, 1939; Grout, 1949) has much empirical standing but needs a cytological clarification (White, 1945; Whiting, 1945). The problems of polymorphism, or caste control within a sex, resist solution in terms of traditional blastogenic and trophogenic concepts used as alternatives (Goetsch, 1937; Gregg, 1942; Haskins & Enzmann, 1945). A broader and deeper range of evidence seems needed.

We believe that the circumstances concerning production of sexes and intra-sex castes in the doryline ants are sufficiently unique to repay careful study. Despite a lively speculative interest of long standing in the literature, coming to grips with this problem has been delayed by certain inherent obstacles to study (Wheeler, 1921). The mode of life of the dorylines made them an inconvenient subject for specialized observation and study, until a suitable methodology had been worked out. This was done in a series of investigations (Schneirla, 1933, 1938, 1944, 1947, 1948) which provided a necessary basis for the present work in method, evidence and theory.

Historical accounts of the early literature concerning doryline sexual individuals are available in papers by Wheeler (1921) and Schneirla (1948). Certain items considered most relevant to our present subject will be mentioned here.

From Marshall's observations, Brauns (1901) reasoned that African driver ants can establish nests only at such times as they breed new queens and males, since, he thought, the bulky larvae and pupae of these forms cannot be carried. Although this hypothesis remains untested

[1] This investigation has been supported through a contract (5T, 164-468) with the Office of Naval Research, Biological Sciences Division. Laboratory studies have been supported in part by a grant from the Committee for Research in Problems of Sex, National Research Council. Through these grants, the help of Mrs. June Esserman, Miss Sarah Lichtenberg, Mrs. Rose Rizki and Dr. John Tafuri was available at various stages in the study of preserved material. The studies carried out in Panama in 1949 by Robert and Frances Brown, as well as those carried out in Trinidad in 1950 by the senior author, were subsidized by grants from the Research Fund of the Council of the Scientific Staff of the American Museum of Natural History. Through the cooperation of Mr. James Zetek, Custodian of the Canal Zone Biological Area, arrangements for the field projects of 1946, 1948 and 1949 benefited indispensably. By his kindness in offering the hospitality of his field station at "Simla," Dr. William Beebe of the New York Zoological Society made possible the field studies of 1950 in northern Trinidad, and through aid from Trinidad Leaseholds, Ltd., with arrangements, the studies were extended to the Guayaguayare section. We are indebted to Dr. Roy Whelden, Haskins Laboratory, Union College, for histological and cytological evidence obtained in his studies on the queens of eciton.

for doryline species in the Old World, it is wrong for New World species thus far investigated. In species of *Eciton (Eciton)* in tropical America, the normal pattern of events involves sessile ("statary") phases at regular intervals, alternating with nomadic phases in which colony activity is maximal and colony emigration is regular (Schneirla, 1933, 1938, 1949). Nomadism and its cessation depend upon social stimulative processes introduced or removed according to the condition of developing broods, but not upon any difficulty in transporting a brood (Schneirla, 1948; Schneirla & Brown, 1950).

Brauns' idea is of interest, however, because of its implication that doryline ants produce their sexual forms under exceptional conditions. Of course, the production of sexual individuals at characteristic times of year and under more or less specialized conditions is common among social insects. Queens are produced in honey bee hives when food is especially plentiful (Grout, 1949), in bumblebee colonies late in the summer (Cumber, 1949), and in temperate-zone ants at times from spring to autumn more or less distinctive of the species (Wheeler, 1913, 1928; Talbot, 1945). As it proves, the dorylines are similar to many other social insects in this respect.

Evidence concerning the production of males accumulated slowly and in piecemeal fashion. Winged males of *Aenictus* sp. were observed in India by Wroughton (1892), and Marshall (Brauns, 1901) witnessed "large numbers" of alates issuing from the exits of a subterranean nest of *Dorylus nigricans*. Hetschko (Mayr, 1886) found "a number" of winged males of *E. (Neiv.) hetschkoi* in nests excavated at Parana, Brazil, and others since have made similar observations on various species of the subgenera *Labidus* and *Neivamyrmex* (= *Acamatus*) in the Americas. Near Austin, Texas, Wheeler (1900) saw winged males "in numbers" leaving a nest of *E. (Neiv.) schmitti* established beneath a stone. Eight days after Gallardo (1915) had dug 50 alate males from a nest of *E. (Neiv.) spegazzinii*, "numerous" males were seen taking off from the same site. "Numerous" enclosed male pupae of *E. (Neiv.) hetschkoi* at an advanced stage of development were found by Hubrich in an underground nest in the northern Argentine and were sent to Bruch (1924) for study. From a colony of *E. (Neiv.) opac. castaneus* observed by Schmidt (Borgmeier, 1948) in Brazil 65 advanced male pupae were taken, 15 of which were freshly emerged; in another, 7 male pupae were found.

Such observations suggest that doryline males appear in distinctive broods, which are fairly large (Gallardo, 1920) and are present only for a limited time in their colonies (Bruch, 1934). This fact was established securely for two species of *Eciton (Eciton)* by Schneirla (1948). Unfortunately, almost no useful information can be gleaned from previous reports of doryline males observed in different parts of the world, relevant to what biological conditions may have attended the production of the respective broods.

Since doryline queens are wingless throughout life, prior evidence concerning their origin and background is very scanty. Unfortunately, the convention developed of terming eciton queens with contracted gasters virgin or young (Gallardo, 1920; Wheeler, 1921; Bruch, 1934), on the incorrect assumption that functional queens must lay eggs or be physogastric more or less continuously. Actually, the gaster of a functional colony queen becomes physogastric only at distinct intervals during the year, and is contracted during intervening periods (Schneirla, 1938, 1944, 1949). It seems to be the rule, as Wheeler (1921) surmised, that normal colonies of *Eciton (Eciton)* and perhaps all doryline species contain only one functional queen.

The previous literature on the American genus *Eciton* contains three records of colonies which apparently had young queens, two cases in the subgenus *Neivamyrmex* (= *Acamatus*) and one in *Eciton (Eciton)*. In a colony of *E. (Neiv.) nigrescens* (= *schmitti*) found by Wheeler (1900) in the vicinity of Austin, Texas, two queens were found among clusters of workers under a stone. The smaller of these was judged circumstantially to be young and virgin; the larger, observed in the laboratory, laid eggs and was evidently the functional queen of the colony. A third queen, intermediate between these two in length and appearance, was found in a tight cluster of workers some days later. It is probable that she was a sister to the other young queen, present all along among the collected ants but previously overlooked in the clusters. In a presumably similar case reported by Bruch (1934), two queens were found in a colony of *E. (Neiv.) hetschkoi* var. *ogloblini* in northern Argentina, October 20, 1932. One was considered virgin because her gaster was contracted (a faulty surmise in itself), the other adult because she laid eggs. The first queen was supernumerary, we believe, and a recently emerged virgin queen (see section 7).

While the first discoveries of what presumably were young queens concerned *Neivamyrmex*, a later finding in the subgenus *Eciton (Eciton)* is circumstantially clearer. In a colony of *E. burchelli* encountered by Wheeler and Emerson in British Guiana on July 21, 1920, in addition to some hundreds of nearly mature male pupae in

cocoons, two "fresh-looking" queens were found moving within masses of workers smoked out from their hollow tree bivouac. Wheeler's comments (Wheeler, 1921) are interesting:

"I believe . . . that the large burchelli colony which Mr. Emerson and I were able to investigate, had already completed the production of its annual brood of workers and soldiers, and that the sexual forms constituted a later or, at any rate, a retarded brood, consisting of a large number of males, all in the same stage and destined to hatch before the end of July, or before the incidence of the dry season, and a very few females, which had hatched before any of the males."

Three of these conjectures find support in our evidence: the distinctness of sexual broods from worker broods, the common age of individuals in a sexual brood, and the presence of only a few queens in the same brood with males. Contrary to Wheeler's (1921) impression, eciton colonies do not produce just one annual worker brood but several, and at regular intervals. This fact was established by the senior author in studies on Barro Colorado I. in the rainy seasons of four different years (Schneirla, 1933, 1938, 1944). Further results show that in species of *Eciton* (*Eciton*) a similar production of worker broods occurs periodically in the dry season as well. In southern Mexico, during the dry months from December, 1944, to May, 1945, 24 colonies representing four species were found with all-worker broods (Schneirla, 1947). There was only one exception.

In early April of 1945 a colony of *E. hamatum* was found near Modelo, Oaxaca, with a brood estimated to contain nearly 2,000 large cocoons. In a sample of more than 500 of these, only male pupae were found in 400 cocoons which were opened, and the remainder were judged identical in a candling operation. However, this was not an all-male brood as reported (Schneirla, 1947), for recently in removing the remaining specimens from cocoons a single queen pupa was found among them (Plate II; Figures 5 & 6).

In a further study on Barro Colorado in the dry season of 1946 (Schneirla, 1949), 10 sexual broods and 60 worker broods were found in the 49 colonies of *E. hamatum* and *burchelli* brought under study. One colony on record for more than four months produced a series of five all-worker broods; another, in the same interval, produced a sexual brood as its second in a series of five (otherwise all-worker) broods. In all samples taken of these sexual broods, only male specimens were found. There was, however, one possible exception. This was the case of colony '46 B-I (*E. burchelli*), in which a supernumerary queen was found during a complex series of events following the emergence of males from cocoons (Schneirla, 1949, pp. 33 f.). A later histological examination showed that this queen was virgin. Altogether, this case closely resembles that reported by Wheeler (1921), in which two "fresh-looking" queens were found among pupal males.

The production of young queens and males was clarified in our investigation of 1948, which provides the main basis for the present paper.

Problem and Hypotheses

We are concerned here with the conditions and processes essential to the production of sexual individuals, and with the production of new queens in particular, in two species of *Eciton* (*Eciton*).

First, we set out to test a hypothesis supported by previous results (Schneirla, 1938, 1948, 1949), namely, that sexual individuals are produced in distinct broods arising through the impact of dry-season conditions upon a functional eciton queen.

Although we expected to find young queens produced together with males in the same dry-season broods, to cover alternative possibilities our investigation extended from the last part of a rainy season through most of the following dry season.

General Schedule; Localities

Field studies were carried out on the behavior and biology of eciton species, chiefly *E. hamatum* and *E. burchelli,* from November 7, 1947, to March 20, 1948. This period included the last five weeks of a rainy season and the first three months of a dry season.

The rainfall pattern during this period is represented by the data in Table 1 (see also Fig. 1, Schneirla, 1949). Although the terminal rains in November and December, 1947, were lighter than is typical for the locality, the dry period which set in after mid-December was normal in its timing, and fairly consistent except for a limited recession in January.

The principal investigation was carried out at Barro Colorado Island, C.Z., with auxiliary surveys in other areas of Panama (Fig. 1, Schneirla & Brown, 1950). There was a survey of 10 days in the Candelaria forest north of Madden Lake, at the end of the 1947 rainy season; another of two weeks in the Tuira R. area of Darien in eastern Panama, about 50 days after the 1947 rains had ended in that area; and one of two weeks in the El Valle area west of the Canal Zone, in early March or somewhat past the middle of the dry season.

Thus, conditions during the terminal rains were studied both at Barro Colorado and one other locality; conditions of the dry season at Barro Colorado and two other localities.

Method and Procedures

Previous publications furnish extensive reports on methods and results of the field investigations of 1946 (Schneirla, 1949) and 1947-1948 (Schneirla & Brown, 1950). These publications are basic to this paper.

All sections of Barro Colorado Island except the southwestern part were patrolled for a maximal coverage of colonies. Colonies of both *E. hamatum* and *burchelli* were studied over considerable periods, with especial attention to colonies with sexual broods (for colony protocols, see Schneirla & Brown, 1950, pp. 276-310, also Figs. 2 and 3). Such long-term studies were aided greatly by a technique for permanently marking colony queens.

Records covered significant features of colony behavior such as the status of raiding and emigration, and of biological condition as indicated by bivouac formation, brood condition and queen's condition. Observations were extended in detail, and supplemented by appropriate tests, for colonies with sexual broods.

Table 1. Rainfall Records for Barro Colorado Island, C. Z., for the Seasonal Transitions of 1945-1946 and 1947-1948

Season	Interval		Semi-monthly totals* (in inches) 1945-1946	1947-1948
Rainy	September	1-15	6.29	4.99
		16-30	3.78	4.54
Rainy	October	1-15	4.37	7.00
		16-30	5.65	6.17
Rainy	November	1-30	7.42	4.33
		16-30	13.18	2.92
Rainy	December	1-15	21.04	4.99
Dry	December	16-31	3.36	0.64
Dry	January	1-15	0.43	0.78
		16-31	0.02	0.86
Dry	February	1-15	0.29	0.02
		16-28(29)	0.03	0.17
Dry	March	1-15	0.10	0.02
		16-31	1.61	0.15

* These records were obtained with a standard rain gauge located in the clearing near the main laboratory building at Barro Colorado I. They are used here through the kindness of Mr. James Zetek.

On Barro Colorado, broods of all colonies under longer study were sampled at intervals of two or three days. To minimize interference with natural events, all samples of sexual broods were held below ½%. Samples for histological study were fixed appropriately in Bouin solution, then stored in 70% alcohol.

In the Candelaria, Darien and El Valle areas, patrolling was scheduled to furnish the maximum possible number of colonies for cross-sectional studies of behavior and biological condition. As a rule, a colony was studied for only a few hours on the day of discovery. In these colonies, large randomized brood samples were taken and, in most cases, the queen was captured for preservation.

Results

1. *Composition and timing of all-worker broods.* In the last weeks of the 1947 rainy season on Barro Colorado I., from November 7 to December 10, only all-worker broods were found in eciton colonies. In 14 colonies of *E. hamatum* investigated, there were 21 worker broods, and in 6 colonies of *E. burchelli,* 10 worker broods. In Candelaria, between December 10 and 19, 9 all-worker broods were found in 7 colonies of three eciton species. No sexual broods were discovered before the dry season began.

As Table 2 shows, none but all-worker broods were found in four previous rainy-season investigations on Barro Colorado (Schneirla, 1938, 1944). In these studies, a total of 103 worker broods was found in 81 eciton colonies.

All-worker broods also are produced by colonies of *E. hamatum* and *burchelli* in the dry season, as may be seen from Table 2. In 17 colonies of four species of *Eciton* (*Eciton*) studied in Mexico in the dry season of 1945, 20 broods in 21 were all-worker broods; in 51 colonies of four species studied on Barro Colorado in the dry season of 1946, 73 broods in 83 were worker broods; and in 41 colonies studied in the present investigation, 57 broods in 67 were worker broods.

Continuation of a periodic brood production throughout both seasons, with all-worker broods predominating, may be considered the rule for colonies of *Eciton* (*Eciton*). In all probability, the spacing of broods is much the same for each species, from season to season, and values obtained in the dry season are close to standard for the year. Our evidence indicates a mode of 36 or 37 days for the cycle in *E. hamatum* and of 33 to 35 days for *burchelli,* with greater variation in the latter (Schneirla & Brown, 1950,

TABLE 2. ECITON BROODS IDENTIFIED IN DRY AND RAINY SEASONS

Year and place	Species	RAINY SEASON				DRY SEASON			
			Type of brood				Type of brood		
		No. of Colonies	All-worker	Eggs; or queen physo-gastric*	Sexual	No. of Colonies	All-worker	Eggs; or queen physo-gastric*	Sexual
1932-1938 (4 seasons) Panama	*E. hamatum*	53	65	4	—				
	E. burchelli	28	38	2	—				
1945 Mexico	*E. hamatum*					6	6	4	1
	E. burchelli					8	11		
	E. rogeri					2	2	1	
	E. vagans					1	1	1	
1946 Panama	*E. hamatum*					31	47	1	4
	E. burchelli					18	23	2	6
	E. rogeri					1	1		
	E. vagans					1	2		
1947 Panama	*E. hamatum*	17	26		—				
	E. burchelli	7	12		—				
	E. conquistador	2	2		—				
1948 Panama	*E. hamatum*					23	33	2	6
	E. burchelli					18	24	2	4
1949 Panama	*E. hamatum*	6	7	1	1				
	E. burchelli	1	1						
1950 Trinidad	*E. burchelli*	26	36	3	1				
	E. vagans	1	2						
TOTALS		141	189	10	2	109	150	13	21

* Nature of brood not established.

Tables 6 and 7). With sexual broods, cycle durations are appreciably shorter in both species.

Examination of many eciton broods under a variety of conditions in both seasons indicates that worker broods tend to be much the same throughout the year. Single worker broods of *E. hamatum* may be estimated at 25,000 individuals, those of *burchelli* at close to 35,000 (Schneirla, 1944), with no evidence for substantial reductions in the dry season. Furthermore, the composition of these broods is very similar in each species throughout the year—a unimodal and continuous polymorphic series not appreciably different in the range of body sizes.

2. *Sexual broods: time of discovery and number studied.* Results for the discovery of eciton broods in the two seasons are summarized in Table 2. It is clear for the localities concerned that sexual broods are to be expected in the dry season but are very exceptional in rainy months.

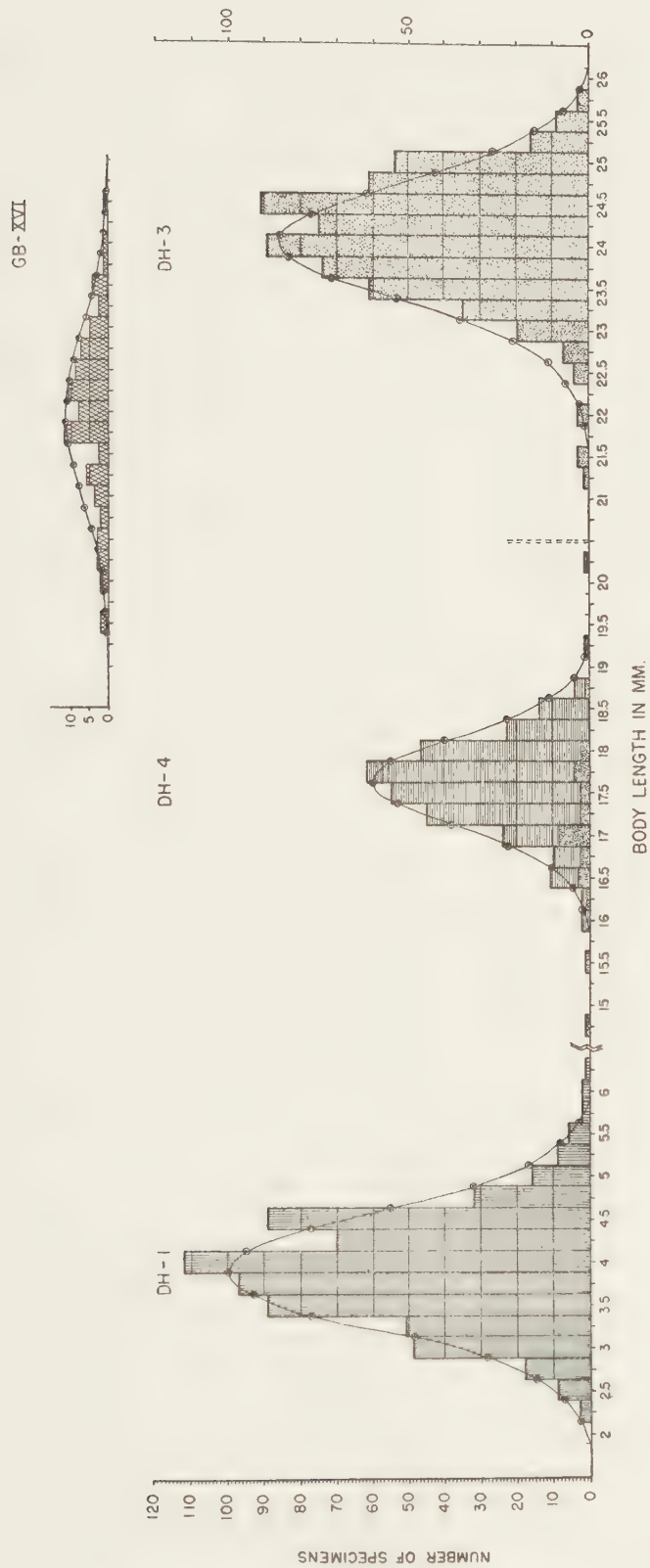
Because extensive surveys have been made in both seasons on Barro Colorado I., results for that locality may be considered basic to our point. In six different rainy seasons there, only one sexual brood was found in a total of 145 broods examined in 108 colonies; whereas in two dry seasons, 14 sexual broods were found in a total of 115 broods examined in 178 colonies. Altogether, in this and other areas in tropical America, 14 percent. of 185 broods examined in the dry season, but only 1 per cent. of 201 broods examined in the rainy season, have been sexual broods.

In the general program of investigation, 23 sexual broods have been found, 15 of them on Barro Colorado Island. In our studies, 12 sexual broods have been discovered in colonies of *E. hamatum,* and 11 in colonies of *burchelli.* Information concerning the specific times and conditions of discovery of these broods will be found in Table 3.

3. *Population characteristics of sexual broods.*

TABLE 3. SEXUAL BROODS STUDIED

Colony and species	Place	Season	Condition of brood when discovered	Period of observation	Composition of brood: Males	Composition of brood: Queens discovered
'45 H-N *E. hamatum*	Coatzacoalcos R. area, Mexico	Dry	Advanced pupal stage; all enclosed	Apr. 23, 1945	Est.: 1,000-2,000	1
'46 B-II-X *E. burchelli*	Barro Colorado Island, C. Z.	Dry	Nearly mature larvae	Mar. 19 to Feb. 20, 1946	Est.: 2,000+	?
'46 B-III *E. burchelli*	"	Dry	Callow males, 100-200 still enclosed	Mar. 1-3, 1946	2,740+ pupa cases	?
'46 B-I *E. burchelli*	"	Dry	Early larval stage	Mar. 2, 1946	Est. 3,000	1
'46 B-IV *E. burchelli*	"	Dry	Alate males in flight condition	Mar. 6 to Apr. 3, 1946	Est. 500 remaining	?
'46 B-V *E. burchelli*	"	Dry	" "	Mar. 29 to Mar. 30, 1946	Est. 1,000 remaining	?
'46 B-VI *E. burchelli*	"	Dry	" "	Mar. 31 to Apr. 20, 1946	Est. 500 remaining	?
'46 H-J *E. hamatum*	"	Dry	Early larval stage	Apr. 3 to 4, 1946	Est. 3,000	?
'46 H-K *E. hamatum*	"	Dry	Larvae, est. two-thirds mature	Apr. 4, 1946	Est. 2,000	?
'46 H-L *E. hamatum*	"	Dry	Callow males in pre-flight condition	Apr. 9 to 10, 1946	Est. 2,000 (Probably high)	?
'46 H-M *E. hamatum*	"	Dry	Callow males in pre-flight condition	Apr. 10 to 11, 1946	Est. 2,000 (Probably high)	?
'48 H-12 *E. hamatum*	"	Dry	Newly laid eggs	Dec. 20, 1947 to Feb. 3, 1948	Est. 15,000+ as eggs; 2,000 at maturity	5
'48 B-XVII *E. burchelli*	"	Dry	Early larval stage	Jan. 23 to Mar. 2, 1948	Est. 2,500	2
'48 H-19 *E. hamatum*	"	Dry	Early larval stage	Jan. 21 to Feb. 20, 1948	Est. 2,000	?
'48 H-27 *E. hamatum*	"	Dry	Early larval stage	Feb. 11 to Mar. 19, 1948	1,619 pupa cases	3
'48 DH-1 *E. hamatum*	Darien, Panama	Dry	Early larval stage	Feb. 14, 1948	Est. 2,500	2
'48 DB-I *E. burchelli*	"	Dry	Callow males; some hundreds enclosed	Feb. 14 to 23, 1948	Est. 3,000	?
'48 DB-II *E. burchelli*	"	Dry	Alate males in flight condition	Feb. 18, 1948	Est. 2,000	?
'48 DH-3 *E. hamatum*	"	Dry	Mature larvae	Feb. 21, 1948	Counted 1,447	8
'48 DB-III *E. burchelli*	"	Dry	Mature larvae	Feb. 27, 1948	Est. 2,800	?
'48 DH-4 *E. hamatum*	"	Dry	Larvae in intermediate stage	Feb. 27, 1948	Est. 2,000	1
'49 H-32 *E. hamatum*	Barro Colorado Island, C. Z.	Rainy	Alate males, est. 8 days post-emergence	Aug. 4 to Sept. 5, 1949	A few hundred	?
'50 GB-XVI *E. burchelli*	Guayaguayare, Trinidad, B. W. I.	Rainy	Mature larval stage	July 10, 1950	Est. 3,000 (unenclosed)	2



TEXT-FIG. 1. Distributions of individuals in large samples representing the sexual broods of four eciton colonies, taken at distinctly different growth stages. Colonies and their samples: '49 DH-1, *E. hamatum*, early larval stage, 598 cases; '48 DH-4, *E. hamatum*, intermediate larval stage, 305 cases; '48 DH-3, *E. hamatum*, at larval maturity, 598 cases; and '49 GB-XVI, *E. burchelli*, at larval maturity, 85 cases. Note the "dwarf" cases of DH-3 (stippled) overlapped with the DH-4 distribution. The respective degrees of significance of fit to a theoretical normal population may be represented by respective acceptance levels of H_0 as follows: DH-1, acceptance at the .01 level when the two largest specimens, both queen larvae, were excluded; DH-4, acceptance at the .1 level when the largest specimen, a queen larva, was excluded; DH-3, acceptance at .05 level; GB-XVI, acceptance at the .3 level of significance.

In our investigations, sexual broods have been studied at all stages from egg to adult, as shown by the summary of records in Table 3. As we shall demonstrate, they are very distinctive as broods, composed almost entirely of male individuals, with a very few queens but no workers. Also, all individuals in a sexual brood begin and end their development within a few days of one another.

Only in one case, that of colony '48 H-12 (Schneirla & Brown, 1950, pp. 283 ff.), have we observed a sexual brood in the egg stage. The queen of this colony was taken from the statary bivouac in a condition of maximal physogastry, her gaster fully as distended as in queens delivering the eggs of eventual worker broods. Her behavior in egg-laying, observed in the laboratory, was closely similar to that of queens delivering worker broods (Schneirla, 1944). The eggs of this brood, viewed en masse in the bivouac when laying was done, seemed quite as numerous as with a worker brood at the corresponding time.

From gross observations of sexual broods at very early larval stages, we have gained the strong impression that such populations are very substantially reduced in number before about the second or third nomadic day (Text-fig. 1). More specifically, in all, 1,376 specimens were taken from this brood in samples (for preservation) obtained on December 21 and 26 from the field bivouac and from lots laid in the laboratory by the queen during her captivity on December 21. Although only a small part of the observed eggs, this number approaches the recorded population *totals* given below for sexual broods in this species at pupal maturity. These preliminary observations should be supplemented by further evidence including population counts at early stages, since the point is an important one.

Successive observations of the same sexual broods at times between early larval stages and pupal maturation, in taking brood samples, indicate that small reductions may take place during that time. A further although limited reduction of the sexual brood population after larval enclosure is indicated by the fact that dozens of empty pupa cases are frequently found in the statary bivouacs. These are usually taken at the border of the brood-free side of the cluster, where the functional queen is located.

Our estimates and counts of mature sexual brood populations show that they are less than 10 per cent. as large as worker brood populations in the respective species (Table 3). For *E. hamatum,* a nearly complete count of mature larvae in the sexual brood of colony '48 DH-3 gave a total of 1,447; a count of pupa cases at the abandoned statary site of colony '48 H-27 gave a total of 1,619, probably close to the actual number in the mature brood. An approximation of 1,500-2,000, or about 7 per cent. of the 25,000 estimated as normal for worker broods, may be made for this species. For *E. burchelli,* our approximation is 3,000, or somewhat more than 8 per cent. of the 35,000 estimated as normal for worker broods.

Batches of alate males found in eciton bivouacs (Table 3) are not reliable as clues to the magnitude of the matured pupal group at emergence. When found in a nomadic colony, such a group represents only one section of the original brood now undergoing a progressive reduction through nightly departure flights (Schneirla, 1948, p. 100).

Although eciton sexual broods are predominantly male, it is probable that a few females are always present. To augment Table 3, further information is given in section 7 concerning the cases in which we have identified young queens in sexual broods, and case résumés follow.

Colony '45 H-N, *E. hamatum.* In a brood sample of more than 500 cocoons containing advanced pupae, all were males excepting one queen pupa (Plate II, Figures 5 & 6). In the field situation, only one sector of the large bivouac cluster was accessible for sampling (Schneirla, 1947).

Colony '46 B-I, *E. burchelli.* An adult, active queen, lighter in coloration than the functional queen of this colony, was found in a distinct cylindrical cluster of workers established at a trail junction well separated from the main bivouac of the colony. This cluster contained hundreds of alate males as well as masses of very young (worker) larvae. Since this supernumerary queen had not been seen in the colony prior to the emergence of the current mature (sexual) brood, and since a subsequent histological examination disclosed no sperm in her receptacle, she may be considered a sister of the males in this brood (Schneirla, 1949, p. 34).

Colony '48 H-12, *E. hamatum.* On January 8, 1948, two days before a statary phase began, four large cocoons were seen being dragged along by workers near the end of a short emigration. As far as could be observed, the population of large larvae was otherwise unenclosed at the time. One of these cocoons, upon examination, proved to contain a mature queen larva just entering prepupation—the others were left with the colony. . . . On January 27, about two days before the first male emergence was established, two callow queens were observed at the statary bivouac; next day, three additional ones were seen. . . . In all, six young queens were

identified in this brood (Schneirla & Brown, 1950, pp. 285 ff.).

Colony '48 H-27, *E. hamatum.* On March 5 and 6, 1948, before any males had emerged, three callow queens were observed at the statary bivouac (cf. Plate III, Fig. 7). From other signs, a fourth may have been present. Two of these young queens were picked up alive at the deserted statary bivouac site when colony division was nearly finished; the third went off with one daughter colony as its queen. Collected on the eighth nomadic day, she was found to have been inseminated meanwhile (Schneirla & Brown, 1950, pp. 304 f.).

Colony '48 B-XVII, *E. burchelli.* On January 27, 1948, probing of the lower margin of the bivouac cluster brought forth two fully formed cocoons. This was before any male larvae were found enclosed, and two days before the colony definitely settled into a statary phase. Both cocoons contained developing queens (Plate I, Figure 1). One was preserved as an early prepupa; the other (Plate II, Figure 4) was raised to the late pupal stage in a laboratory nest (Schneirla & Brown, 1950, p. 306).

Colony '48 DH-1, *E. hamatum.* In a preserved sample containing an estimated one-third of this brood (see section 4 and Text-fig. 1), the two largest specimens were found to be queen larvae, all others male (Schneirla & Brown, 1950, p. 313).

Colony '48 DH-3, *E. hamatum.* During a complete examination of this brood upon its removal from the colony bivouac in the field, all larvae were found naked with the exception of 14 which had begun to spin cocoons. Eight of these were queen larvae (Schneirla & Brown, 1950, p. 315).

Colony '50 GB-XVI, *E. burchelli.* In this case (see Table 3), found in Trinidad, the bivouac cluster contained a large sexual brood nearly at larval maturity. The brood was inspected part by part as the bivouac was demolished, and all larvae were found unenclosed with two exceptions. One of these, in a complete cocoon, was found to be a queen prepupa (Plate I, Figure 2); the other, in an incomplete cocoon, was a somewhat less advanced queen prepupa.

Since we have identified young queens as members of sexual broods in eight different cases, their development in the same broods with males seems well established. No young queens at any stage of development have been taken except in connection with male broods. Young queens are very few in number, at least after an early larval stage, and easily overlooked. Our largest number of identified callow queens in a brood is five, the next largest, three; of identified mature larvae eight, and next largest, four. How many potential queens may be present at early larval stages, prior to the second nomadic day, cannot be said at this time.

Once suitable methods had been developed, young queens were found with regularity in sexual broods, although always in very small numbers. Early queen larvae were found in large samples from the sexual broods of colonies '48 DH-1 and DH-4 by taking the largest specimens, and all others were male; they were found as mature larvae or prepupae in colonies '48 H-12, B-XVII, DH-3, and '50 GB-XVI, on the expectation that queen larvae become enclosed before males; they were found as emerged callows in colonies '48 H-12 and H-27 on the expectation that queens complete their development and leave their cocoons before males. Thus our earlier failure to find queens in certain sexual broods (Schneirla, 1949) cannot be accepted as evidence that none were present.

4. *Distribution of individuals in sexual broods.* Except for a few queens, eciton sexual broods contain only males. A useful conception of individual differences in these broods is given by three samples taken from different colonies of *E. hamatum* (Text-fig. 1) studied in Darien, R.P., in February of 1948. Each of these samples was randomized, and each very large. Fortunately, the three brood populations when found and sampled were at very different stages of larval development, as may be seen in Text-fig. 1. Circumstances indicated that colony DH-1 was in its second day of a nomadic phase when an estimated one-third of its early-stage larval brood was taken; colony DH-4 was entering the last third of a nomadic phase when an estimated one-sixth of its intermediate-stage larval brood was taken; and colony DH-3 was in its last or next to last day of a nomadic phase when nearly one-half of its mature larval brood was taken (Text-fig. 1). (Except for small Bouin-fixed lots, all three brood samples were preserved in 70 per cent. alcohol). Large samples from the sexual brood of colony '45 H-N (*E. hamatum*) at an advanced pupal stage and that of colony '50 GB-XVI (*E. burchelli*) at larval maturity have been available for comparison.

Studies of the larval samples have included measurements of total body length, body width at fifth segment and dimensions of leg buds. Measurements were made in a standardized manner with micrometer calipers under low-power magnification, with separate anterior and posterior measurements to correct for body arcing in larval specimens.

Since no evidence has been found for poly-

morphic specialization in any male population, data on body length will serve for a general comparison of these cases. The three samples of different sexual broods at early, intermediate and late stages of larval development, are represented in Text-fig. 1. The distributions of the DH-1 and DH-4 brood are unimodal and fit a theoretical normal-frequency distribution curve to a fairly good approximation (see legend, Text-fig. 1). In contrast to these distributions, that of the DH-3 sample is somewhat skewed and exhibits a distinct although minor bimodality. Since no other sexual brood closely observed at larval maturity (e.g., H-12, H-27) has departed from a unimodal pattern, we are considering DH-3 a special case. This judgment is supported by the fact that the samples of sexual broods from both colony '50 GB-XVI, taken at a stage of larval maturity (see Text-fig. 1) and '45 H-N, taken at an advanced pupal stage, closely approximate a normal-frequency pattern.

We have found only two deviations from the normal-frequency pattern in sexual brood populations sampled after an early larval stage has been reached (i.e., after their colonies have passed the second nomadic day). The first is a limited departure, theoretically expected in all eciton sexual broods. It occurs at the upper extreme of the size distribution, involving the young queens. In the DH-1 sample the two queens found were the longest, and in the DH-4 sample the one queen found was the longest in the series. With these omitted, the normal-frequency fit is a closer one in each case. (The DH-3 sample cannot be considered a randomized sample with respect to the upper extreme, since, as mentioned in section 3, 14 specimens were removed which had begun to spin. Eight of these were queens, the others probably among the largest of the male larvae.[2] It seems probable that the male populations of eciton sexual broods, considered after they have passed an early larval stage, tend to approximate a smoothly graduated normal-frequency distribution.

The DH-3 male distribution clearly deviates from the others in two particulars. Not only is the principal bulk of the curve definitely skewed upward, but there is also a cluster of small individuals well separated from the main body of the population. All of these last individuals were seen at the time of collection, but more than a dozen of them were quickly bundled away by workers. A randomized sample of the remaining smallest members of the population is represented in Text-fig. 1, where it falls within the size range of the DH-4 sample. Clearly, the case of colony DH-3 calls for separate study.

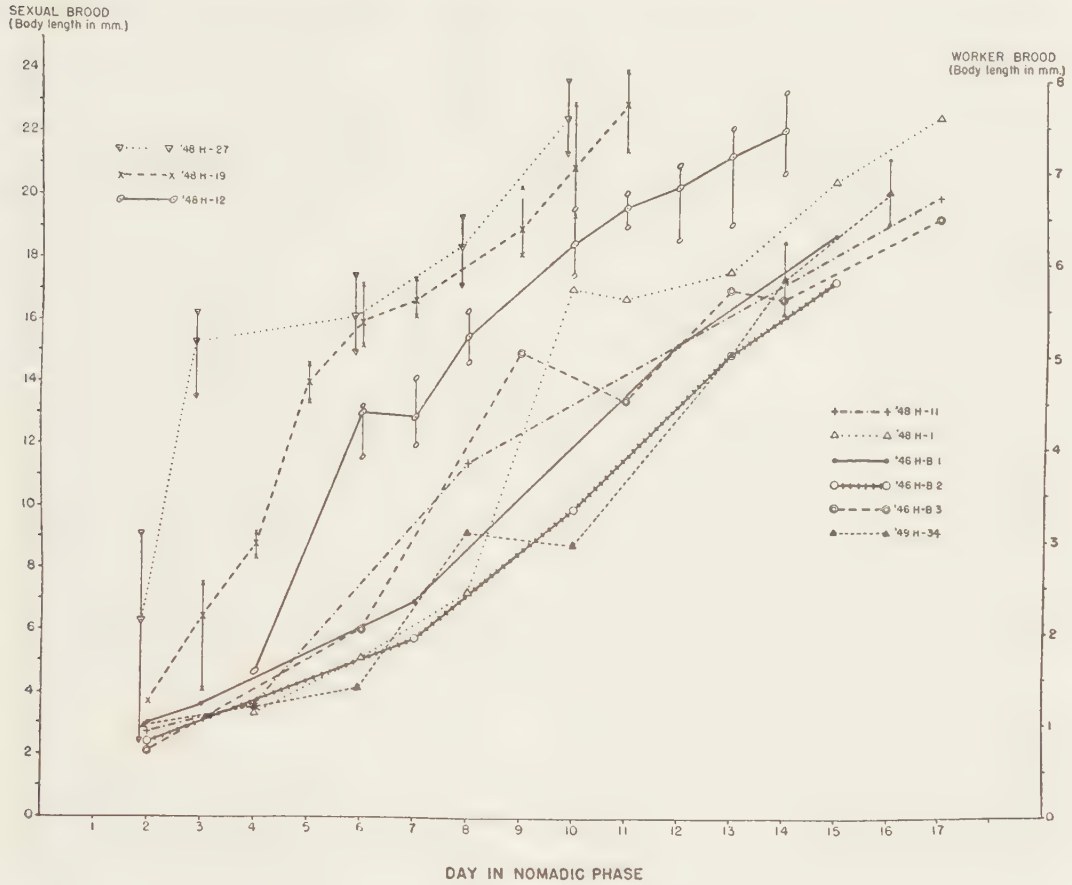
5. *Course of larval development.* The sexual broods of three colonies of *E. hamatum* and two of *burchelli* investigated on Barro Colorado were sampled periodically through the principal part of their larval development, on alternate days when possible. As a rule not more than 12 specimens were taken in a sample. The three sexual broods of *E. hamatum* are represented in Text-fig. 2 in terms of the means and ranges of over-all body lengths in the respective samples. For purposes of comparison, mean body-length curves obtained from larval worker broods of various colonies of *E. hamatum* are also presented in Text-fig. 2. It should be noted that each curve begins at the nomadic day on which the represented brood was first sampled —for example, the H-27 brood was first sampled on the second nomadic day and H-12 on the fourth day. All curves end with the last sample taken before larval maturity.

In the developmental curves for the three sexual broods, an early marked acceleration of growth is notable, followed by a more gradual approach to maturity. The initial acceleration is seen first in H-27, next in H-19 and last in H-12. It occurs in the H-27 brood from the second to the third nomadic day, roughly, but in the H-12 brood not until the fourth day of the phase. In the records for the two sampled *burchelli* broods, an abrupt rise of similar nature begins about the third nomadic day in both cases (cf. '46 B-I, Schneirla, 1948, 1949).

In the slow trend of these sexual broods toward maturity, after the initial stage of rapid growth, brood differences are indicated in Text-fig. 2. Although the terminal phases are gradual in all three cases, and similar in slope on the whole, progress in the H-12 brood seems to have slowed somewhat toward the end, especially as compared with H-27.

From the results represented in Text-fig. 2, it may be seen that the trend of development is distinctively different in sexual broods as compared with all-worker broods of *E. hamatum.* During the first third of the nomadic phase the larval worker broods exhibit a low rate of development, in contrast to the early spurt of larval sexual broods. The curves also indicate that when an increase appears in the rate of larval-worker development, it is considerably slower than the earlier increase in sexual larvae. It appears that larval development is accomplished in a different course and more rapidly in sexual broods than in worker broods.

[2] An effort was made to raise these for preservation at respectively different advanced stages, as with the specimens taken from colony '48 B-XVII on Barro Colorado. Unfortunately, kept under the variable conditions of field travel, all died without pupating.



TEXT-FIG. 2. Growth rate of three larval sexual broods (upper left) and six larval all-worker broods (lower right) of *Eciton hamatum,* represented by curves for average over-all body lengths in successive samples taken in the nomadic phase. Ordinate scales of the curves are approximated for equivalence in height at the point of larval maturity of sexual and worker broods. Colony identifications for sexual broods are given at the upper left; colony identifications for all-worker broods at the lower right of the figure. Individual samples ranged in magnitude from 10 to 30 individuals in the sexual broods (for which the ranges of body lengths are shown by vertical lines), and from 500 to 1,500 in the all-worker broods, in which, for clarity, expressions of variability are omitted except for the σ's of the last two samples of the H-34 brood.

Although we are not well equipped with evidence concerning early larval development in sexual broods, it is apparent from the figure that by the second nomadic day sexual larvae approximate a body size close to the average size of worker larvae at maturity (i.e., at nomadic days 15-17). In section 4 we noted that size differences among male larvae are not absolute but relative at this time, since a normal-frequency distribution is approximated (e.g., in the brood of colony DH-1, Text-fig. 1). Also, such relative differences evidently are maintained throughout larval development, since similar distributions are obtained at various later stages. The magnitude of the difference at larval maturity may be expressed in the following way: a randomized sample of 341 mature male larvae (alcohol preserved) of *E. hamatum* (DH-3) displaced 71 cc. of water, but a randomized sample of 341 mature worker larvae displaced only 4 cc. At maturity, therefore, male larvae have roughly 17.8 times the body volume of worker larvae, presumably a crude indication of the ratio of their tissue bulks. According to calculations based on this ratio, in *hamatum* a brood of 25,000 mature worker larvae would have the same bulk as 1,405 mature male larvae. Actually, a total of 1,447 larvae was counted in the sexual brood of colony DH-3.

6. *Duration of developmental stages in sexual*

broods. It is very probable that the eggs of any sexual brood are laid in a single series, which has a definite range of variation and a normal, unimodal pattern of individual differences at later stages of development. Our evidence favors the assumption that individual differences in degree of maturity depend upon the order in which brood members are laid as eggs, and that these relative positions are maintained throughout development. On this basis, the growth stages in any brood may be described properly with reference to the estimated mid-point of egg delivery as origin.

From previous observations concerning physogastry and egg-laying in the eciton queen (Schneirla, 1938, 1944, 1949), the mid-point of egg-delivery may be set tentatively at 10 days before the end of the statary phase, the duration of the entire egg-laying process at about six days. Since age differences within a brood probably are relative, as indicated above, the mid-point of egg-delivery is accepted provisionally as the expressed origin time of the brood.

The values given in the first column of Table 4 represent hypothetical statements of the inclusive time from egg-laying through hatching to the early stage of larval development attained when the statary phase ends. Accepting the value of 10 days for this interval is a necessary expedient which should not exclude a variability from brood to brood, no doubt greater in *burchelli* than in *hamatum.* The end of a statary phase is conditioned upon the emergence of a mature pupal brood, an occurrence more delimited in time for colonies of the latter species (Schneirla, 1938). Successive broods are not exactly synchronized even in *hamatum,* and in some cases nomadism may begin after a shorter post-hatching interval than in others. Thus, when nomadism began, the H-12 and H-19 sexual broods were less advanced than that of H-27 (Text-fig. 2), possibly for this reason.

Termination of the nomadic phase is taken as a rough indication of larval maturity in sexual as in worker broods, since it coincides with the prevalence of cocoon-spinning in both cases. In sexual broods, the beginning of nomadism, as well, is a turning point for the larval brood, since then or shortly thereafter this brood undergoes a sharp increase in rate of development not seen in worker broods (Text-fig. 2). With this interval added, the values in the first two columns of Table 4 give 18-19 days as a rough statement of developmental time from egg-laying to larval maturity in the sexual brood of *E. hamatum.* It appears, then, that this interval is from 7 to 10 days shorter for sexual broods in this species than for worker broods. In *burchelli,* the difference is similar in direction, but less.

Duration of the ensuing statary phase may be taken as a close approximation of the time required for development from larval maturity to pupal maturity, since the beginning of this phase coincides with enclosure and its end with emergence of the same brood. From data in the fourth column of Table 4, it appears that this terminal period of development has much the same duration in the cases of sexual and of worker broods in both species. In view of the much greater bulk of the sexual-brood young, their similarity in pupation time with worker young is a notable fact.

As Table 4 indicates, the total duration of development in the sexual broods of *E. hamatum,* under the conditions of our study, was close to 40 days, or about one week less than the developmental time of worker broods in this species. The difference is smaller in *E. burchelli.* In both species, the difference may be referred to a shorter period of larval development in sexual than in worker young, in contrast to nearly equal times for development within cocoons.

7. *Precocity of the queens in sexual broods.* In six of the ten cases in which sexual broods were taken in 1948, queens in very small numbers were present with the males (Table 3). In all of these cases, the queens appeared to be more advanced than the males in development. In the early-stage larval brood of colony DH-1, the two queen larvae found were larger than any males; and in the intermediate-stage larval brood of colony DH-4, the only queen larva found was larger than any male. In colonies DH-3, H-12 and B-XVII studied in Panama in 1948, as well as in GB-XVI found in Trinidad in 1950, one or more queens reached larval maturity and became enclosed ahead of the males. In colonies H-12 and H-27, three or more queens had emerged as callows before any callow males were found. A precocious development of queens in sexual broods is indicated.

Instances in which young queens have been found in this program are summarized briefly in section 3. In the case of colony '48 H-12, a contrast of queens and males is possible at two well separated times in development. First, at a time when all male larvae evidently were still unenclosed, four similar dark cocoons were observed. One of these, when opened, was found to contain a queen prepupa which had completed its larval maturation in advance of the males. This, no doubt, was also true of the three uncollected specimens. Later, just before the statary phase ended, four active callow queens

TABLE 4. DURATION (IN DAYS) OF DEVELOPMENTAL STAGES IN WORKER AND SEXUAL BROODS

Species and colony	Developmental stage: Mid-point of egg-laying to early larval stage (i.e., to end statary phase)		Early larval stage to maturity and enclosure (i.e., through nomadic phase)		Prepupal and pupal development (i.e., statary phase)		Total developmental time	
	Worker broods	Sexual broods	Worker broods	Sexual broods	Worker broods	Sexual broods	Worker broods	Sexual broods
E. hamatum								
'46 H-B	(10)*		16		21		47	
" "	(10)*		17		20		47	
" "	(10)*		16		20		46	
'48 H-11	(10)*		17		18		45	
'48 H-15	(10)*		17		20		47	
'48 H-18	(10)*		18		19		47	
'48 H-12		(10)*		13		21		44
'48 H-27		(10)*		12		21		43
E. burchelli								
'46 B-I	(10)*		10		20		40	
" "	(10)*		10		21		41	
" "		(10)*		8		21		39

* Inferred value.

were seen in this colony before any evidence could be found of male emergence from cocoons.

A study of brood samples from colonies '48 DH-1 and DH-4, taken in Darien, suggests that queen precocity holds from an early stage of larval development. In each of these instances, queen larvae were largest in a sample otherwise composed of hundreds of male larvae. Three further cases point to queen priority in reaching larval maturity. In an examination of the brood of colony DH-3 as the bivouac was demolished literally strand by strand, 14 larvae were found which had begun to spin. (Unfortunately, a plan to keep most of these specimens alive for preservation at further stages was unsuccessful). Eight queen prepupae were identified among them. At the time these individuals were already well advanced in making their cocoons, virtually all of the male larvae were still active and unenclosed. The males, although naked, were nearly ready to spin, as indicated by the expulsion of a large wad of viscid fluid from each when plunged into hot water.

On the assumption of queen precocity we were able to capture the first larval specimens of queens ever taken in *E. burchelli* (Schneirla & Brown, 1950). When colony '48 B-XVII was in its next to last nomadic day with a larval sexual brood, probings into the cluster brought forth only naked male larvae, with two exceptions. Intrusions into the lower border of the bivouac at length disclosed two complete cocoons, each within a tight bolus of workers. One of these cocoons, opened soon afterward at the laboratory, yielded a queen in the prepupal stage (Plate I, Figure 1). The second was placed with workers in an artificial nest, where the workers clustered over it closely or lugged it about intermittently in their circular column. When opened nine days after it was collected, this cocoon contained a well-formed queen pupa (Plate II, Figure 4). Thus, both of the enclosed specimens were queens, and both were more advanced in development than any observed male larvae in the same brood.

Similar evidence was obtained in colony GB-XVI, *E. burchelli urichi,* studied by the senior author in Trinidad. When found in late afternoon, this colony was engaged in a vigorous raid based on a large cluster within the broken shell of a hollow log. When a sexual brood close to larval maturity was found within the bivouac, steps were taken to look for enclosed specimens. In a brood estimated to contain 3,000 larvae, all of those observed were naked with the exception of two enclosed specimens, each within its own compact bolus of workers. One had completed the spinning of a cocoon closely similar to those of the two prepupae of colony '48 B-XVII, and on removal was found to be a queen prepupa. The other, within a thinner case evidently still incomplete, also was a queen prepupa. As may be seen in Plate I, Figure 2, the

latter was smaller and evidently less mature than the specimen in the completed cocoon. Both of these specimens evidently were ahead of the males in development, since all males observed in this brood were still naked, active and unstraightened.

In three instances, fully emerged young queens have been found in broods of still enclosed male pupae. In the colony of *E. burchelli* observed by Wheeler and Emerson (Wheeler, 1921), two active ("fresh looking") queens were found, doubtless both callows which had emerged before any of the nearly mature male pupae. In our study, the earlier eclosion of queens was established clearly in two colonies of *E. hamatum,* and was suggested by circumstantial evidence in colony '46 B-I, *E. burchelli.*

Detailed records are available from two colonies of *hamatum.* When colony H-12 was passing its 18th day (January 27) of a statary phase with an enclosed sexual brood, a fully emerged, active young queen was seen within a cluster of workers close to the main bivouac. She was removed for preservation. On the evening of the same day, two further callow queens were seen in the bivouac vicinity, one outside the cluster but near it, and another in the bivouac wall. A fourth was observed later the same evening, in a cluster at some distance from the main bivouac. These queens were all readily identified as callows by their light orange-yellow coloration. All four moved about freely and vigorously, except as restrained by workers clustered about them or following them closely, at a time when no emerged males could be found in the bivouac. Next morning (January 28) small numbers of eclosed alate males were observed; male emergence accelerated during the day, continued on January 29 and reached its virtual completion late in the evening. In this case, the first queen seems to have emerged about two days before any males, and all of the later queens evidently preceded all except a few initial male eclosions.

In colony H-27, the first callow queen (Plate III, Figure 7) was observed on the evening of March 5, the 17th day of the statary phase, in a small cluster near the bivouac; the second on the following day, at noon, also in a small separate cluster of workers; the third a few hours later, exposed in the center of a thick group of workers. The first signs of male emergence were not observed until late afternoon on March 7. Male eclosion continued at an accelerated rate to its completion on March 10th, when the colony moved from the site in the evening. In this case, not only the first callow queen to be observed, but evidently one or both of the others as well, reached pupal maturity and emerged from their cocoons before any of their brother males.

8. *Conditions of production of sexual broods.* In studies on Barro Colorado during the rainy months of six different years, in a total of 108 colonies, 153 broods were identified, and only one of these was a sexual brood. In the forested areas of the Caribbean region, where annual rainy and dry seasons were well differentiated, production of all-worker broods seems almost invariable in colonies of *Eciton* (*Eciton*) during the rainy season.

Results stated in section 1 show that a regular production of worker broods is the basic pattern of the dry season as well; however, in dry months the succession is interrupted in some of the colonies by the appearance of a bisexual brood (Table 2). During the final rainy weeks of 1947 preceding the onset of dry weather, 24 colonies of *E. hamatum* and *burchelli* were studied on Barro Colorado and in the Pequeni area of Panama, with a total of 38 all-worker broods but no sexual broods discovered. But subsequently, in 41 colonies studied in the 1947-1948 dry season, 11 sexual broods were found in addition to 59 worker broods, on Barro Colorado and in Darien. And on Barro Colorado during the dry months of 1946, 49 colonies of the two species had a total of 71 all-worker broods and 10 sexual broods. In the areas of study, with limited exceptions to be considered, sexual broods evidently are specific to the dry season.

The connection of sexual broods with dry weather has a striking illustration in the case of colony H-12. During November and early December of 1947, this colony was studied during the time it produced two successive all-worker broods. These were the last weeks of the 1947 rainy season (Table 1), and on December 10 (when we left the Island for another area) ground moisture was plentiful. When we returned on December 20 the situation was sharply different: rainfall had stopped abruptly about one week before, lower vegetation was dry, and the forest floor had lost moisture to the extent that ground cracks were widespread.

On December 22, or about ten days after dry weather had set in (see Table 1), colony H-12 was rediscovered, then in a statary bivouac within the blind hollow of a large open log shell, in a dry hillside clearing exposed to the south. From the developmental status of the pupal worker brood, the colony was judged to have spent about two weeks at this site before its discovery. This estimate agrees with previous

phases of the colony (Schneirla & Brown, 1950), and would allow for a statary phase of 20 days before a new nomadic phase began on December 28.

In the December statary phase a sexual brood was initiated. The H-12 queen was physogastric when taken from the bivouac on December 22, but had evidently finished delivering the main part of her current batch of eggs. In one sample of nearly 100 eggs taken from the mass already laid, many well-advanced embryos and some minute larvae were found, which with graduated signs of development in the remainder indicated that egg-laying must have been going on for a few days. This queen, as observed during a captivity of three hours in the laboratory, was similar in egg-laying and related behavior to other queens of this species studied in the last stages of an egg-delivery episode (Schneirla, 1944).

On December 26 when the bivouac was next examined, from the queen's behavior and from the reduced size of her gaster, together with the size of the large brood mass, it was apparent that delivery of eggs must have ended. Nomadism began on December 28 when, after carrying out a three-system raid during the day, the colony completed an emigration early in the night (with a large, newly emerged brood of callow workers). On December 31, when this colony was rediscovered (and identified by means of the queen's mark), its young brood was at once seen to be a sexual brood.

From all the circumstances, this colony must have entered a statary phase about December 8, or only two or three days before dry weather began in the general locality. Thus it is highly probable that during the principal time of physogastry and egg-delivery, colony H-12 and its queen were subject to conditions of marked heat and drought in the known bivouac location, sharply in contrast to circumstances prevalent in the microclimate during the final weeks of rains, when this colony initiated two successive worker broods.

For reasons to be clarified in the discussion, we propose that the first half of a statary phase is the critical time for events determining whether a brood is to be sexual or all-worker in make-up. In the light of this assumption, let us examine our evidence on sexual broods found in the dry seasons of 1946 and 1948.

In Table 3 there is a general record of the cases in which sexual broods were found in the 1946 and 1948 dry seasons. In each case, a judgment has been made of the developmental status of the brood at the time of discovery, based on a comparison of the brood sample with evidence from continuous studies of brood development in the species (cf. Text-figs. 1 & 2).From these considerations in relation to evidence on the duration of development presented in section 6, each brood has been traced inferentially to the time of its initiation. The estimated times of inception for the respective sexual broods discovered in the two dry seasons are given in Table 5.

The investigation in the 1946 dry season (Schneirla, 1948, 1949) began early in February. As may be seen in Table 3, 10 sexual broods were found between February and early April, but none thereafter to mid-June. Of these cases, six were in colonies of *burchelli* and four in *hamatum*. It is interesting to note in Table 5 that the critical brood-initiation times (according to our hypothesis) fall before February 8 in all six *burchelli* broods, but after that date in all *hamatum* broods. This may be a true species difference, dependent upon conditions in the particular season and year.

It seems relevant here that *burchelli* colonies when statary often bivouac in hollow trees at considerable distances from the ground, whereas *hamatum* colonies usually remain on or close to the ground. In the 1946 dry season, of 27 recorded statary bivouacs in *burchelli*, 10 were at ground level, 6 within one meter, and 11 at heights between one and ten meters from the ground; of 36 recorded statary bivouacs in *hamatum*, 25 were at ground level, 10 within one meter, and 1 at two meters. Atmospheric conditions affecting the statary bivouacs of these two species must have been very different, as a result. On Barro Colorado in late 1945, rainfall was exceptionally heavy, as indicated by a December total more than twice the average of a 15-year record for that month (Schneirla, 1949, Fig. 1). In January and February of 1946, however, rainfall was sparse, accounting for a persistent atmospheric dryness in the forest during the daytime. On the other hand, in most parts of the island, retention of ground moisture was excellent even to the middle of February. In the first two weeks of the 1946 season, *burchelli* colonies in their elevated statary sites may have been more effectively exposed to drought than *hamatum* colonies in their sites close to the ground.

In 1946, rains continued into early January, then stopped abruptly on Barro Colorado. From the estimated times of brood initiation in Table 5 it is evident that colonies B-I, B-II, B-III and B-IV (*E. burchelli*) must have initiated their sexual broods before January 20. Thus, in four of six colonies of this species found with sexual broods in that season, the event had its inception within three weeks after intensive dry weather

TABLE 5. INFERRED TIMES OF INITIATION OF ECITON SEXUAL BROODS STUDIED DURING TWO DIFFERENT DRY SEASONS

(H—colony of *E. hamatum*; B—colony of *E. burchelli*)

Season	Time interval						
1945-1946	Dec. 16-31	Jan. 1-15	Jan. 16-31	Feb. 1-15	Feb. 16-28 (29)	Mar. 1-15	Mar. 16-31
		B-IV	B-III B-II-X	B-VI B-V B-I	H-K	H-J	
Total		1	2	3	1	1	
1947-1948	H-12 DB-II	H-19 B-XVII DB-I	H-27 DH-3 DH-1	DH-4 DB-III			
Total	2	3	3	2			

began. Comparably, in 1948 the sexual brood of colony H-12 was initiated during the first three weeks of dry weather, and the sexual broods of colonies H-19 and B-XVII evidently were initiated not long thereafter, in early January.

We propose that some, if not all, of the conditions for sexual-brood initiation are met when a colony enters its first statary phase after dry weather has begun. From this hypothesis, when a drought begins suddenly and is maintained, more eciton colonies should produce sexual broods than when dry weather begins gradually and continues brokenly. It seems significant that in 1948 only four eciton colonies with sexual broods were found, as compared with ten in 1946, although nearly equal totals of more than 50 colonies of the two species were studied on Barro Colorado in these two dry periods. Somewhat more variable environmental conditions during the first half of the dry season in 1948 than in 1946 may have been responsible.

In an area presenting a variety of microclimatic conditions, as does Barro Colorado with its many ravines and hills, chance differences in statary locations may be critical for sex control in broods. In 1948, although colony H-19 initiated a sexual brood during a statary phase which began on January 31, colony H-18, which began a statary phase at nearly the same time, had a worker brood instead. And colony H-23, which must have begun a statary phase in December, 1947, not long after H-12, initiated a worker brood while the latter colony had a sexual brood. It seems important that whereas both colonies H-12 and H-19 passed these statary phases in distinctly dry forest glades well exposed to air currents, colonies H-18 and H-23 were located in more humid and better sheltered places. In *burchelli*, colonies B-XII and B-XVII had coincident statary phases early in January; however B-XII was situated in a deep and moist interbuttress niche where it initiated an all-worker brood, whereas B-XVII had a more exposed cluster three meters from the ground in a broken tree trunk, where it initiated a sexual brood. Our records contain other contrasts of this type, but no contradictory instances.

In Table 5 it is seen that most of the sexual broods found on Barro Colorado in 1946 and all of those found in 1948 were initiated before the end of February, or during the first third of the dry season. In 1946, a routine search for colonies continued from early February to mid-June; in 1948, a similar search continued nearly to the end of March. If sexual broods were initiated to any extent in the last weeks of the dry season, it seems also that evidences of them should have been found in the investigations of four different years when routine searching was carried out during May and June. The one trace of a late dry-season inception in *Eciton* (*Eciton*), a dealate male found in a colony of *E. hamatum* on June 10, 1932, must have developed in a brood initiated before the end of April, i.e., before the end of the dry season.

Our Darien survey of 1948 was scheduled on the assumption that in an area where the dry season begins abruptly with persistent drought thereafter, initiation of eciton sexual broods is

confined largely to the early weeks.[3] The dry season in lowland Darien typically begins late in December and is continuous until late April, and 1948 was a typical year. Our survey was carried out during the last two weeks of February when, according to the above hypothesis, a maximum of colonies should have sexual broods in advanced stages of development. Results fully justified this expectation, since in a total of eight discovered colonies, six colonies had sexual broods. These broods ranged from an early larval to a post-pupal stage, and, as Table 5 indicates, must have been initiated after the beginning of dry weather in late December. Although a repetition of the survey in March or April, desirable as a control, unfortunately was not possible, results for Barro Colorado Island (Table 5) indicate the probable outcome.

9. *Exceptional (rainy-season) sexual broods.* As Table 2 shows, our records cover a total of 191 identified broods in five species of *Eciton* (*Eciton*) studied during various rainy seasons in Panama and other areas. In this long series only two cases, or 1 per cent., were sexual broods. In contrast, in a total of 172 broods of four species studied in the regular dry season, 22 broods (i.e., about 13%) were sexual. In a tropical area with well-differentiated seasons, it appears that sexual broods are produced only exceptionally in the regular season of rains.

There are two apparent exceptions in our records, to which in all probability the case discovered by Wheeler and Emerson (Wheeler, 1921) should be added. The first of our special cases was the *hamatum* colony ('49 H-32) found with a presumably remnant alate male brood at Barro Colorado Island on August 4, 1949, by Robert and Frances Brown (Table 3). This colony terminated a nomadic phase on August 12, which provides a basis for inferring the developmental stages of the sexual brood. With July 26 taken as the approximate date of emergence of the sexual brood, from considerations outlined in section 6, the statary phase in which this brood was initiated may be presumed to have fallen roughly from June 7 to 27, with egg-laying about June 13 to 21. Normally the rainy season begins during May in this locality (Schneirla, 1949, Fig. 1). In the 1949 rainfall records for Barro Colorado, precipitation was regular and normal in amount from early May to the end of the rainy season in December, with the exception of early June. From the records reproduced in Table 6, it may be seen that in the intervals June 3 to 7 and June 14 to 18, rainfall was sparse in the daytime hours. It therefore is possible that an interval of hot, dry weather may have affected colony and queen at the time postulated as critical for brood initiation.

Our second special case, as described previously, was colony GB-XVI (*E. burchelli urichi*) found in southeastern Trinidad on July 10, 1950, during a nominal rainy season. From the fact that this sexual brood was then only about one day short of larval maturity, the statary phase of its production may be inferred as from about June 10 to 30, and the duration of egg-laying roughly established as from June 17 to 23. Fortunately, rainfall records were available from a locality only about 10 miles from where this colony was found, and close to the heavy forest.[4] Precipitation was somewhat irregular but appreciable in amount through May, but a significant change came after the first days of June, as represented in Table 7. After June 9 there ensued an interval of more than three weeks in which days were almost altogether rainless, hot and clear, with rainfall restricted to scattered light showers at night. It is possible, as the table indicates, that the sexual brood later found in colony GB-XVI was initiated within this dry interval.

The sexual brood found by Wheeler and Emerson in a *burchelli* colony at Kartabo, British Guiana, was close to pupal maturity on July 21, 1920, near the end of a short semi-annual rainy period. From considerations presented in section 6 and summarized in Table 4, it seems probable that this brood was initiated during the first three weeks of June. In the absence of published data, Dr. William Beebe was asked about precipitation in the Kartabo area during the months of May through July in 1920, when he was in continuous residence at the station. His reply, based on his notes for that season, was that after an irregular but appreciable rainfall through May, the month of June and especially its first half had been very dry and clear, followed by consistent rains until near the end of July. Thus, the interval of sexual-brood inception in the recorded colony may have coincided with a distinct dry period following a series of rains.

[3] A comparison of the daily march of atmospheric changes at Yavisa in Darien, as reported by Breder (1946), with conditions at Barro Colorado, shows that at Yavisa air temperature rises more rapidly in the morning and reaches a considerably higher peak at midday with a lower trough in humidity, and drops more slowly in the afternoon than at Barro Colorado.

[4] These records were obtained with a standard funnel-type rain gauge operated at the Beach Field station of Trinidad Leaseholds, Ltd., and are used here through the courtesy of Mr. Peter Highgate, Chief Engineer at the station.

TABLE 6. RAINFALL RECORDS FOR BARRO COLORADO I., C. Z., FROM MAY 15 TO JUNE 30, 1949, WITH ESTIMATED TIMES OF SEXUAL BROOD INITIATION IN COLONY '49 H-32, *E. hamatum*

Date	Rainfall in inches: 12 P.M. to 6 A.M.	6 A.M. to 12 A.M.	12 A.M. to 6 P.M.	6 P.M. to 12 P.M.	Inferred colony events	
May 15		.01	1.78	.16		
16		.01	.06	.06		
17			1.28	.01		
18	.01		.01			
19						
20			.48	.07		
21	.28	.01	.06	.02		
22	.02	.22		.10		
23	.10		.32			
24		.01				
25	.12		.25	.04		
26			.01	.02		
27	.06		.81	.03		
28			.22	.05		
29		.01	1.06			
30			.17	.01		
31	.01					
June 1		.01	.19	.14		
2	.01	.04	1.52	.03		
3	.01					
4						
5		* .07		.03		
6	.09	* .21				
7						
8	.02	.01	.91		(Statary phase	
9			.11	.02	inferred,	
10	.01	†1.10	‡ .75	.03	June 8-27)	
11	.21	.19			"	
12		.01	.89		"	
13			‡2.24	.27	"	
14	.10			.15	"	(Egg-laying inferred,
15			.05		"	June 14-21)
16					"	"
17	.01			.34	"	"
18	.01	† .05		.01	"	"
19	.04	* .46	‡ .09	.01	"	"
20			.06		"	"
21		.01		.18	"	"
22	.01				"	
23	.04		.01		"	
24	.01				"	
25				.02	"	
26			.38		"	
27	.01	.19	.20		"	
28		.01	.44			
29			.41	.94		
30	.01		.62			

* All before 8:00 A.M.
† Mainly before 8:00 A.M.
‡ After 2:00 P.M.

It is probably no accident that in all three of our ostensibly exceptional cases, in which an eciton colony produced a sexual brood during a period of nominally rainy weather, dry periods of appreciable duration occurred at about the time when brood initiation may be inferred. It seems possible that these were not actually exceptional cases, but really equivalent to the case of colony H-12, in which egg-production and laying were established in close coincidence with the first two weeks of a regular dry season.

Discussion

In these eciton species the pattern of life is much the same throughout the year, in that great all-worker broods are produced at regular intervals and colony behavior oscillates synchronously between the nomadic and statary conditions. In the dry season, neither more arduous environmental conditions nor difficulties in getting an adequate haul of booty prevent a continuation of this pattern. The most striking reaction of *Eciton* to the dry season involves the production of fertile individuals and the colony sequels to this event.

In American tropical areas with well-marked seasons, in which our results have been obtained, broods appear periodically in rainy months with large populations of workers alone but no reproductive individuals whatever (section 1). This is also the case in the dry season, with the exception of a single bisexual brood in some of the colonies (section 2). Under the conditions of our study, production of sexual broods in eciton is an event specific to the dry months. Our findings provide a basis for understanding how these exceptional broods are produced, not only in tropical areas having distinct seasons (sections 2 and 8), but also in regions without well-defined seasons (section 9).

For the two terrestrial species of *Eciton* (*Eciton*) we have studied, a sexual brood is a distinct population of young developing from eggs laid by the same queen, which contains a small number of potential wingless queens and a large number of potential winged males (section 3). Briefly summarized, the demonstrated characteristics of this event are: seasonal timing (sections 2, 8, and 9); apparent restriction to one such brood per colony per season (sections 2 and 8); a dimorphic makup, with few females and many males (sections 3 and 4); a fractional population size as compared with all-worker broods, fairly constant for the species (section 3); a precocious development and emergence of queens (sections 4 and 7); a distinctly shorter period of larval development, with a different time rate of change, than in worker broods (sections 5 and 6); and graduated individual differences in size approximating a normal-frequency distribution (sections 3 and 4). To account adequately for these characteristics, it seems necessary to postulate factors concerning egg-production and egg-delivery in the queen as well as factors in colony behavior affecting brood development, distinct from conditions in the population of worker broods.

Our evidence favors the hypothesis (Schneirla, 1948) that the initial impact of dry-season conditions upon colony and queen specifically causes sexual broods. In the first place, such broods tend to appear early in the dry season (sections 2 and 8), each one as a single episode in a regular series (otherwise of all-worker broods), and furthermore, it is probable that no colony has more than one such brood in a season. The critical time in the cycle for this effect seems to be roughly the first half of a statary phase, when the queen becomes gravid and delivers a single large batch of eggs (section 8), During this interval the queen may be susceptible to extrinsic conditions which somehow determine the sex of this brood.

Evidence presented in sections 8 and 9 indicates that specific environmental conditions as well as a colony susceptibility are involved. The chances that many colonies in an area will be exposed to the necessary extrinsic conditions within a theoretical time limit after the onset of dry weather evidently depend upon what colonies may settle into statary phases at nesting sites where dry-weather conditions prevail. Thus colony '48 H-12 on Barro Colorado, after producing two successive all-worker broods during the last rains in 1947, almost coincidentally with

Table 7. Rainfall Records for Beach Field, Guayaguayare, Trinidad, from June 1 to July 12, 1950, with Estimated Times of Sexual Brood Initiation in Colony GB-XVI, *E. burchelli*

Period	Total rainfall in inches	Developmental stage of brood
June 2- 5	3.83	
" 6- 9	3.02	(Statary phase inferred, June 10-30)
" 10-13	0.25	
" 14	0.30	
" 15-18	1.15	(Egg-laying inferred, June 17-23)
" 19-22	2.00	
" 23-26	0.85	
" 27-30	0.85	
July 1- 4	0.55	
" 5- 8	0.90	Larvae mature, July 10-11
" 9-12	0.70	

the onset of dry weather entered a statary phase at a site where drought conditions soon prevailed. This colony seems to have been maximally exposed when susceptible, and a sexual brood resulted. Certainly, the *general* prevalence of dry weather in an area does not *alone* condition such broods in all colonies. Other colonies, which became statary at nearly the same time as colonies producing sexual broods, but which entered more humid and better sheltered sites, produced all-worker broods.

A greater coincidence of eciton sexual broods was expected in the Darien lowlands, where dry weather begins almost coincidentally with Barro Colorado but is more intensive. In Darien, most of the eciton colonies discovered in the last two weeks of February had sexual broods, doubtless initiated within the first month of the dry season (Table 5). On Barro Colorado more than 50 colonies of two species were discovered in the same season, but only four had sexual broods. There, with a more variable microclimate and rainfall pattern, chances evidently were considerably less than in Darien that any one colony would meet the necessary conditions in its first statary phase after dry weather began. These considerations suggest a somewhat different pattern of inter-colony mating in eciton colonies of these species, according to the conditions of terrain and climate in the area.

The abruptness with which dry weather begins and the uniformity with which it dominates the microclimates of an area seem critical for the occurrence of sexual broods there. Conditions on Barro Colorado in the dry season of 1946 would appear to have been more favorable than in 1948 in this respect, for 10 sexual broods were found in 1946 but only four in 1948, in comparable surveys. A related question concerns why six sexual broods of *E. burchelli* found in the 1946 dry season evidently were all initiated before any of the recorded cases in *hamatum*. The answer apparently depends upon a species difference, whereby *burchelli* when statary tends to occupy elevated sites far more frequently than *hamatum*. Under the climatic conditions prevalent in this area in 1946, with the ground moister than usual but with a very dry daytime atmosphere, early in the dry season *burchelli* colonies must have been more frequently and fully exposed to dry conditions than *hamatum* colonies (section 8). In 1948, with the forest floor much drier from the start of dry weather, no species difference of this kind was obtained.

Apparently, eciton sexual broods may be produced at any time of year, provided a susceptible colony encounters the necessary extrinsic conditions. Three cases have come to light in which sexual broods were produced outside the regular dry season of the locality (section 9). In each of these cases, a distinct period of dry weather may have coincided with the time when a colony presumably became statary and initiated a sexual brood.

Specifically, a sexual brood may be expected when a colony with functional queen, acclimated to rainy-season conditions, is subject to persistent dry-weather conditions in the first half of a statary phase. In our study, sexual broods were initiated most frequently in the early part of the regular tropical dry season (section 8). We find indications that relatively few colonies have sexual broods after the first third of the dry season has passed, and that some colonies have only worker broods in given dry seasons. Hence it is possible that through a variable or a gradual introduction to dry-season conditions, a queen and colony may become acclimated by degrees early in the season and thereby protected in some manner from maximal dry-weather effects encountered later on. Or, on the other hand, once the effective extrinsic conditions have accounted for production of an exceptional brood, an inhibitory effect of some kind may oppose a repetition in the same season. We have many records in which sexual broods were preceded and followed by worker broods, but none of two successive sexual broods in the same colony, or of two from the same colony in the same season.

A considerable precision in this event in *Eciton*, with stable properties according to species, is indicated by the manner in which sexual broods occur and by their population characteristics (sections 2, 3, 4, and 7). *Eciton* seems to have far greater precision than most other insects, both in the ratios of dimorphic individuals produced at one time by any one colony and in the manner of their appearance. In most other insects, protandry (i.e., prior appearance of males) is the rule, usually somewhat variable, as in *Trigona* (Schwarz, 1948). The opposite condition, queen precocity, is relatively rare and seldom as precise as in *Eciton*. In *Eciton*, so far as we know, queens never appear in the same brood with workers, but always as a precocious minority in a brood otherwise containing only males.

Considering the high degree of uniformity which evidently prevails throughout colonies of a species in *Eciton*, the pattern is indeed a striking one. For example, it is probable that a functional queen of *E. hamatum* normally produces about nine successive all-worker broods

before a sexual brood may interrupt the annual series. On the Dzierzon assumption that female-producing eggs are fertilized eggs, this queen must therefore produce a rough total of 200,000 or more fertilized eggs, in separate lots at 36-day intervals, before a break to a dimorphic brood occurs. On the same assumption, the major part of a sexual brood, namely the males, might be considered the result of some major interruption in the fertilization of matured eggs. This would be a time-limited change, from which a queen normally recovers fully to the condition in which fertilized eggs once more are produced invariably in each great brood of the series.

At first sight the sexual-brood event might seem attributable to a depletion of sperms in a queen, with a possible recovery through refertilization. It is true that male-producing eggs are laid intermittently with an increasing frequency by elderly queens in certain ants (Goetsch & Käthner, 1937) as well as by honeybee queens when over-aged (Grout, 1949) or low in sperms (Laidlaw & Eckert, 1950). This hypothesis does not seem to fit *Eciton,* since it would lead us to expect sexual broods of variable makeup produced at almost any time of year, and not seasonally conditioned broods of a consistent dimorphic population pattern, preceded by full-sized all-worker broods. Moreover, all functional eciton queens thus far examined histologically, whatever the season of capture, have been found with ample supplies of sperms in their receptacles. From our evidence, it would appear that *any* functional eciton queen may produce a sexual brood, provided the necessary extrinsic conditions are effective when queen and colony are susceptible.

The state of affairs in *Eciton* in this respect is not unrelated to conditions in other insects. It is well known that reproductive variations, including changes in the sex ratio, may occur in many insects under the influence of extrinsic conditions (Wigglesworth, 1939; Flanders, 1939). A seasonal production of fertile individuals is common in insects, although its mechanism is poorly understood. In ants, males and queens are ordinarily produced at times characteristic of the species, early in the temperate-zone summer in some and later in others (Wheeler, 1913; Talbot, 1945); male-producing eggs are usually laid by honey bee queens in the autumn (Vandel, 1931), the season when males and fertile females ordinarily are produced by bumblebees (Cumber, 1949). Insect metabolic processes are known to be delicately responsive to changes in environmental temperature and humidity in particular (Uvarov, 1931; Chapman, 1931; Mellanby, 1935; Ludwig, 1945), and the reproductive processes of many are very sensitively affected by ecological conditions (Alpatov, 1932; Wigglesworth, 1939). Specifically, the ovaries in queens of numerous ant species have been found to vary in function according to relatively slight changes in individual metabolic conditions (Wheeler, 1913; Ezikov, 1923). It is not surprising that reproductive processes in doryline queens show a sensitivity to seasonal extrinsic changes.

Theoretically, we may characterize the extrinsic effect in the case of *Eciton* as an adequate dry-season impact, its terminal organic result a temporarily sustained inhibition of egg-fertilization in the functional queen. This relationship is undoubtedly less direct and plastic than in some of the solitary Hymenoptera, in which a comparable process occurs promptly by reflex response to specific extrinsic stimuli (e.g., size of host), or in the honey bee queen, in which contact with a large comb cell typically elicits the laying of an unfertilized egg, a small comb cell a fertilized egg. However, the mechanism in *Eciton* may not be dissimilar to that outlined theoretically by Flanders (1939, 1950) specifically for the honey bee.

What intervening variables may be set into play by seasonal extrinsic factors to cause exceptional reproductive changes in the eciton queen? We are limited to speculation. The phenomenon may involve a rather direct and reflex-like process set up by the action of specific atmospheric changes upon the queen; it may be an outcome of more subtle metabolic changes (e.g., water reduction) attributable to extrinsic conditions; or it may be even more indirect, with the inclusion of social factors. To illustrate the last hypothesis, one possibility is that the critical extrinsic conditions may first act upon the general population, perhaps by lethargizing the workers sufficiently to reduce trophallactic stimulation for the queen below the level essential for facilitation of insemination processes.

Whatever its *modus operandi,* the phenomenon has certain general properties which may be inferred from our findings. Properties of stability and perhaps of complexity are suggested by an apparent latency in onset which would seem to impose a precise limitation on fertilization at the beginning of each exceptional series. A process with a definite threshold is indicated by the all-or-none manner in which insemination apparently stops. A process of more than simple reflex characteristics, but with a stable and persistent organic mechanism, is indicated by the continuation of the non-fertilization condition once it is in force. A metabolic

sustaining condition of a temporary and all-or-none character, opposed by conditions normal to the nomad-statary cycle, is suggested by evidence for a seasonal adaptation against a repetition of the episode. In all of these respects the phenomenon occurs in a markedly precise way, indicating great stability of the causal factors in the species.

Because the first-laid eggs are presumably fertilized, they develop into females; also, through their prior emergence in the colony, they have a certain advantage for competition in the colony trophic situation. There is at present no reason to believe, however, that these first-delivered members of the potential sexual brood are different genetically or in nutrient resources from the corresponding members of a potential all-worker series. In both cases, the initial eggs evidently are fertilized, hence develop into females. However, we have no evidence for different rates of egg-production in the two broods, hence no apparent basis for a differential absorption of nutrient material, as postulated by Flanders (1946) to account for queen-worker specialization in other social insects. If no differences exist in the nutrient content of initial members in the two egg series, the development of queens in the one case and major workers in the other must be attributable to trophic processes in the colony situation, effective after laying. A genetic differentiation seems unlikely here.

Interesting consequences follow from the postulation of potential sexual- and worker-brood series which are equivalent in timing and in number at delivery into the colony. Dimorphic differences within the sexual brood presumably are due to the non-fertilization of all but an introductory part of that egg series. At the moment of fertilization, however, similar graded differences presumably exist through each series, perhaps in the nutrient content of eggs as dependent upon their order of maturation. This condition, suggested by the absorption theory of Flanders (1945), would establish a basis for the graduated differences arising within each type of population. A stable basis of this sort for individual differences is suggested by the high degree of similarity we have found in the unimodal bisexual populations from an early larval stage, and by a comparable situation in all-worker broods. Graduated differences of such a description, established prior to laying and later amplified trophically through development in the colony, may furnish a basis for degrees of variation among individuals in both series. It is presumed that genetic factors effective through fertilization admit polymorphic differences among females up to a limit dependent upon the trophic advantages available to each individual. It is also presumed that non-fertilization excludes such differences in the male series.

Very different potentialities for colony reaction appear to exist in all-fertilized and mainly-unfertilized series of eciton eggs produced in separate broods. Between the time of laying and our first glimpses of the larval broods at the start of nomadism, some catastrophic change must be imposed upon the potential bisexual brood to which the entire all-worker brood seems to be immune. The apparent result is that the sexual-brood population is reduced to a small fraction of its number at laying, a fact of greatest importance for the eventual character of the sexual brood.

To account for this reduction, two alternative hypotheses may be offered. The first is that unfertilized eggs may be inferior in viability to fertilized eggs, so that most of them fail to pass some critical stage of early development (e.g. hatching). An alternative hypothesis concerns the possibility of an extensive cannibalism by workers based on specific chemotactic properties of unfertilized eggs. Some shortcoming in odorous properties, such as a deficiency in surface fluids, might cause unfertilized eggs to be treated like booty. Or on the other hand, some discriminable property of unfertilized eggs might cause workers to lick and handle them excessively, and thereby consume many of them in the process. This might indirectly increase the casualties among potential queens in particular. That the trophallactic reactions of licking and handling, when intense and exaggerated, can readily become transformed into feeding, has been made plausible by Wheeler (1928). Under given trophic conditions eciton workers readily consume the brood, as we find when whole colonies are kept in the laboratory with insufficient food.

Whatever the processes of brood-reduction may be in this instance, it is clear that they must operate on a chance basis through the population, since close approximations of a normal-frequency pattern are obtained with the survivors (Text-fig. 1). Susceptibility to the eliminative processes therefore would appear to have a chance relationship to position in the brood series. Furthermore, these processes must operate in a comparable manner and to much the same extent in all potential sexual-brood populations of a species, since we find that the magnitude of finally matured populations is characteristic of the species.

The elimination of the greatest part of the potential bisexual brood, which apparently occurs in *Eciton,* seems to be critically important

for shaping the condition of the eventual brood. Through the postulated reduction processes the number of potential food-competing individuals is brought to a relatively low and relatively constant magnitude and thereby a predictable over-feeding of all survivors is insured. Perhaps the organic matter made available as a by-product of this process contributes part of the diet of the survivors in the early stages of larval development. An early over-feeding, which may be augmented from this source, must account for the distinctive growth superiority of a sexual brood as compared with a potential worker brood at the beginning of nomadism.

The queen larvae, with the remaining survivors of the eciton sexual brood, exhibit a remarkable early spurt in development not seen in the case of worker broods (section 5). As a result of such differences and the constant individual over-feeding on which they must depend, members of the sexual brood reach larval maturity within about one week less than the time required by worker larvae. At that stage they have more than twice the body length and nearly 20 times the body volume of the largest worker larvae at maturity. The mature queen larvae are not only much larger, but are clearly differentiated from worker larvae in both their external and internal morphology.[5]

The potential queens, as compared with their counterparts (i.e., individuals developing from first-laid eggs) in the potential worker brood, thus enjoy a considerable advantage. It is safe to say that the few potential queens leading a sexual brood series are enormously over-fed (and probably also hyperstimulated) throughout their development in comparison with the relatively low food limit which must be imposed upon the corresponding (soldier-producing) members of a potential worker brood. In contrast to the queen, the worker or neuter-female social insect is generally considered a product of chronic inanition during development, a "starvation form" (Wheeler, 1928). In its general outlines the eciton situation appears to resemble that of the honey bee, for which there is evidence (Rhein, 1933; Melampy, et al., 1940; Haydak, 1943; Kuwabara, 1948) that genetically equivalent fertilized eggs may produce workers or queens, depending upon whether food supplied during post-hatching development is sufficient to bring the larva to the queen threshold. Evidence bearing upon the importance of over-feeding for production of queens as against workers has been reported for ants by Wesson (1940), and for *Trigona* and *Lestrimelitta* species among stingless bees by Kerr (1946, 1950).

A sexual brood must be considered an interactive agent in the functioning of its colony, basically similar to a worker brood in this respect (Schneirla, 1938). With both types of brood in the early larval stage, a great batch of newly emerged callows sets off a nomadic phase (Schneirla, 1948, 1949). These callow adults feed voraciously for a few days, and must furnish a heavy food competition to the young larval brood. In the case of worker broods, this factor must play a large part in holding down the growth rate during the first few nomadic days while the callows retain heavy appetites. It is probably no accident that an initial slow growth rate in the larval worker brood (see Text-fig. 2) coincides with a period of maximal intra-bivouac activity and feeding in the callows. Matters are different for the sexual-brood larvae, which accelerate strikingly in growth rate during the period of callow-worker maturation and feeding. These larvae are already rather large at the start of nomadism, and plainly more attractive to workers than are worker larvae at that stage, hence are individually more successful than worker larvae in the food competition. Also, since by that time the sexual brood has been reduced to a fraction of the size of a worker brood, large-scale feeding can proceed among its members despite the competition of voracious callows.

It seems clear that the distinctly shorter time required for larval development in a sexual brood is attributable to a high growth rate sustained by maximal feeding, as compared with underfeeding in worker larvae. It is probable that, during a larval stage only about two-thirds as long as with worker broods, a sexual brood consumes roughly the same total of food as does a worker brood of far greater numbers. These very different broods are roughly the same in their total tissue bulks at larval maturity, although the population of a sexual brood then is considerably less than 10 per cent. as large as that of a worker brood. This would suggest that in these two types of broods approximately the same amount of food is distributed among very different numbers of growing individuals.

Studies both under field and laboratory conditions indicate that at most stages of development a more extensive and intensive trophallactic relationship holds between workers and sexual brood than with a worker brood. This

[5] Although nearly 2,000 ovarioles have been found by Dr. Roy Whelden in a queen prepupa of *E. burchelli*, and 1,200 by Dr. Harold Hagan in a functional queen of this species, few or no homologous structures are found in worker larvae of the species (see also Holliday, 1904).

difference is revealed in a variety of ways. For example, getting brood samples from a bivouac usually is more difficult with a sexual brood, because of a greater reactivity of workers to these larvae and a greater tenacity in clinging to them than to worker larvae. In the bivouac, each of the large male larvae is held within a group of workers, the center of a distinct zone of stimulation and activity. The intensity of this relationship undoubtedly is greatly magnified with queen larvae. Observed in laboratory nests, the workers are found much more responsive to male larvae than to worker larvae of about the same size. They cluster more tenaciously about sexual larvae, spend more time licking, touching and shifting them about, and drop food upon them more frequently than with worker larvae. During the colony emigration at night, the complexity and high pitch of activity in transporting the bulky male larvae emphasize the strong energizing effect of this brood upon the colony. This is exemplified in the formulation of living "ant roadways" which become more prominent in the colony movements as a sexual brood advances in larval development (Schneirla, 1948). Correspondingly, daily raids show a striking increase in scope and in numbers of participants as the nomadic phase wears on.

Evidence on the developmental status of queen larvae (sections 4, 5, and 7), indicates that from an early stage they must enjoy a relative advantage over the male larvae in their stimulative potency for workers. Direct observations support this conception of the young queens as dominant trophallactic agents. Even when the queen larvae have become enclosed in cocoons, they are individually the centers of greater commotion among the workers than are any of the male larvae. Actually, their trophallactic advantage over the males appears to increase in time, very possibly with the advent of distinctive processes (e.g., secretory) augmenting their attraction for workers. There is no question that any one of the newly emerged queens is a far more powerful attractive and excitatory agent among the workers than is any one male (Schneirla & Brown, 1950).

The emergence of most or all of the young queens from their cocoons before the males, evidently typical in the ecitons, is a fact of the greatest importance for the final outcome. Also very significant for the colony reaction is the existence of gradations in behavioral status among the young queens, with a clearly superior attraction for workers exerted by the most precocious of this small group. These and other principal aspects of the eciton sexual brood serve as stable prerequisites to the occurrence of colony division and related events.

Although the trophallactic relationship of a sexual brood to its colony is basically similar to that of a worker brood, it differs from the latter in important ways. A sexual brood exerts a general excitatory effect upon workers which promotes nomad-statary processes essentially as does a worker brood (Schneirla, 1938, 1944, 1949). Each type of brood exerts a total excitatory effect adequate to maintain nomadic function while it is in the larval stage of development. With sexual broods this phase is shorter in both investigated species than with worker broods, which have a longer stage of larval development. The statary phase, on the other hand, shows no reliable difference with the two types of brood, which are nearly the same in the duration of their post-larval development. In both cases, the emergence of a mature pupal brood raises colony excitation to the threshold of nomadism. With sexual broods, however, colony excitation is definitely higher at this time than with worker broods. This high level of arousal proves crucial for the manner in which the first emigration and its unique related events take place.

Hence, there is an important qualitative difference in the colony reaction to these two types of broods. An accentuated attraction of workers to the sexual brood may be in force from the egg stage, with a consequent intensification of brood and colony relationships. The composite effect of this type of brood in the colony is different in nature from that of a worker brood, judging from a contrast in the bivouac situation of these broods. From an early larval stage the placement of a sexual brood suggests a nascent split in the worker population, in that many workers, through a persistent affiliation with the brood, tend to avoid the functional queen and workers associated with her. Through this expanding process of counter-attraction, there arises a complex state of affairs which reaches a head only with the emergence of the sexual brood. In this entire process, the developing queens may be considered nuclear.

In a forthcoming paper, a further consideration of these events will demonstrate that the seasonally conditioned appearance of eciton sexual broods has reproductive consequences not only in the production of fertile individuals, but also in the rise of new colonies.

Résumé and Conclusions

In the two investigated species of *Eciton* (*Eciton*), fertile individuals are produced in distinctive annual broods which typically are

initiated early in the dry season. The apparent cause is an impact of dry weather upon queen and colony, which in some direct or indirect manner may effect a temporary inhibition of fertilization during a periodic episode of egg-production and delivery.

Acclimation to the dry-season impact seems possible, either insulating the queen against a repetition of the sexual-brood episode in the same season, or preventing the occurrence of this episode if exposure has been gradual.

Possibly a slight initial latency in the action of extrinsic factors on the queen's reproductive processes may account for the laying of a few fertilized eggs to start each series, with queens developing from these eggs through a consistent overfeeding in the colony. These queens are precocious with respect to their brother males at all stages of development.

In *E. hamatum,* a mature sexual brood contains only about six new queens together with 1,500-2,000 males; in *E. burchelli* there are likewise only a few new queens with as many as 3,000 males. Either a relatively low viability of unfertilized eggs, or cannibalistic inroads of workers against these broods, reduces them to fractional proportions at an early stage of development.

A radical reduction of total numbers in a sexual brood at an early stage permits the overfeeding of all survivors. Consequently in this brood there is a marked early spurt in larval development not shown in worker broods, and the larval stage is appreciably shorter than in worker broods. The time required for post-larval development is nearly the same in the two types of brood. Total developmental time in *E. hamatum* is about 40 days with bisexual broods, in contrast with about 47 days required by an all-worker brood.

That a stable set of conditions governs the production and development of any sexual brood is indicated by the fact that large randomized samples taken from early larval stages of development tend to approximate a normal-frequency pattern. Since the total tissue bulk of a sexual brood at larval maturity approximates that of a worker brood at the same stage, the influence of rigid limiting factors governing colony food-economy may be suspected.

A more intensive trophallactic relationship holds between the worker population and a sexual brood than when an all-worker brood is present. The developing queens have a central role in a process whereby a nascent division arises in the colony, a process developing through the maturation of a sexual brood. This paper therefore is preliminary to a further study on the processes of colony division in these army-ant species.

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EXPLANATION OF THE PLATES

Plate I

Fig. 1. Specimens of mature larvae from the sexual brood of *Eciton burchelli,* colony '48 B-XVII (see Table 3). *From the left:* (1) cocoon (approximate length, 24.3 mm.) containing a mature queen larva, from which, 10 days later, the pupa represented in Plate II, Figure 4, was removed; (2) a mature queen larva removed from a cocoon nearly identical with that of '1'; (3 and 4) male larvae taken at the same time, still unenclosed.

Fig. 2. Lateral view of specimens from a sexual brood of *E. burchelli* (colony '50 GB-XVI —see Table 3) taken at the mature larval stage. *From the left*: the first and third specimens are queen larvae (approximate lengths, 24.6 and 23.7 mm.), the former completely enclosed at capture, the latter partially enclosed. The other specimens, both mature male larvae, were naked at capture (approximate lengths, 24.2 and 23.7 mm.).

Fig. 3. Below: ventral view of the two queen larvae. (N.b.: Coloration modified as result of fixing in Bouin's solution).

Plate II

Fig. 4. *From the left*: dorsal, lateral, and ventral views of a pupal queen of *Eciton burchelli* (colony '48 B-XVII—see Table 3). This specimen was originally taken as a mature larva which had completed its enclosure and was entering the prepupal stage (see Plate I, Figure 1). It was kept with workers in the laboratory for 9 days, during which it developed into the pupa shown in this figure (approximate length, 19.6 mm.).

Fig. 5. Dorsal view of pupal queen of *Eciton hamatum* (center, over-all length, 18.6 mm.) with two male pupae from the same brood (over-all lengths, 17.5 and 16.3 mm.).

Fig. 6. Ventral views of the same specimens (colony '45 H-N—see Table 3).

Plate III

Fig. 7. Virgin queen (left) and callow male of *Eciton hamatum* (colony '48 H-27—see Table 3). When this photo was taken, the queen was at six days and the male roughly at three days post-emergence. Over-all length of queen (less antennae), 19.6 mm.

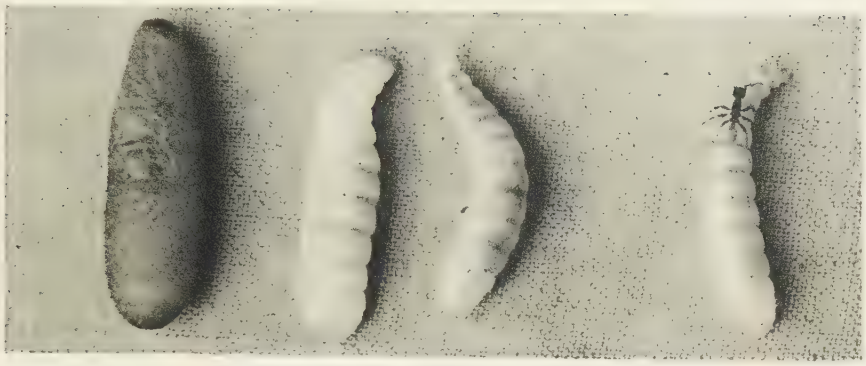

FIG. 1.

FIG. 2.

FIG. 3.

SEXUAL BROODS AND THE PRODUCTION OF YOUNG QUEENS
IN TWO SPECIES OF ARMY ANTS.

FIG. 4.

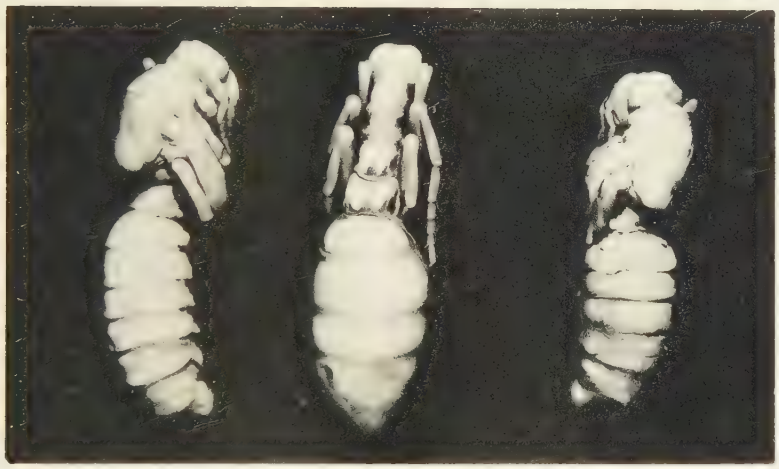

FIG. 5.

FIG. 6.

SEXUAL BROODS AND THE PRODUCTION OF YOUNG QUEENS
IN TWO SPECIES OF ARMY ANTS.

FIG. 7.

SEXUAL BROODS AND THE PRODUCTION OF YOUNG QUEENS
IN TWO SPECIES OF ARMY ANTS.

3

Spectral Effects on the Growth Rate and Endocrine Histology of the Teleost, *Astyanax mexicanus*

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American Museum of Natural History and New York University

(Text-figures 1-4)

IT has been shown by Rasquin (1949) that prolonged maintenance of *Astyanax mexicanus* (Fillipi) in total darkness prevented normal functioning of the endocrine system. A depressed pituitary condition followed, together with thyroid hyperplasia, reduced gonads and retarded and deformed somatic growth. In the present experiment, *Astyanax* were maintained in daylight, under colored filters, in order to compare possible differential effects of specific regions of the visible spectrum with those produced by a lightless environment.

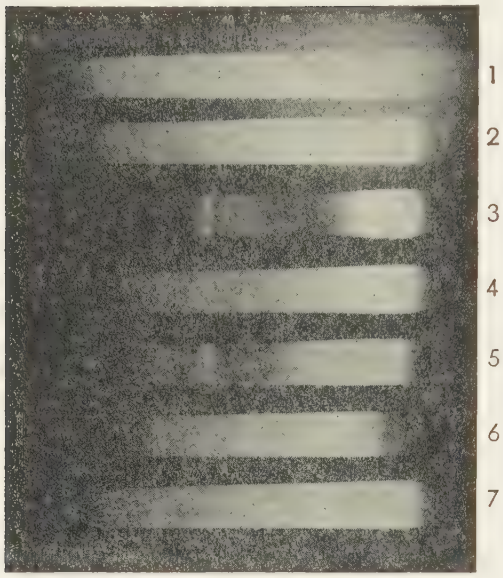
No previous studies directly concerned with wave length effects on the endocrines of fishes could be found in the literature, although the spectral influence on the growth of young salmon (Yung, 1881; Crawford, 1930) and on fish behavior (Kawamoto & Takeda, 1950) and color vision (Warner, 1931; Walls, 1942) has been described.

The experimental work reported here was carried out in the laboratory of the Department of Fishes and Aquatic Biology of the American Museum of Natural History. The author wishes to thank Dr. Charles M. Breder, Jr., and Priscilla Rasquin of this department for reading and criticizing the manuscript.

MATERIALS AND METHODS

Thirty fish of the same spawning, approximately two months old, and of about the same size, were equally distributed among five adjoining aquaria. These tanks, 16¼ by 8½ by 10 inches high, with glass sides and a slate bottom, contained only water. They stood on a stand six feet below the glass skylight of the aquarium room. All sides and the top cover of four of the tanks were covered respectively with red, yellow, green and blue cellophane sheets, with an opaque cardboard between the ends to eliminate influences between adjacent tanks. One tank, the control, was left without cellophane covering. The yellow cellophane was manufactured by the Sylvania division of the American Viscose Corporation, and the red, green and blue, by the du Pont Cellophane Division. The extent to which the transmission of the filters varied was determined by spectrophotometric analysis, and is considered in the interpretation of the significance of the results. Daylight served as the only source of light. Aquarium room temperature during the nine-month experimental period (July through March) varied from 65 to 80 degrees F. All of the fish received a balanced daily diet of a standard dried food (Aronson's formula, 1949) which contained 12 percent. protein, 2 percent. fat and 32 percent. carbohydrate.

Monthly growth measurements were obtained as follows: the distance from the tip of the snout to the anal opening was recorded for length values, and the widest point in the body region for greatest depth values, measured at right angles to the axis of the fish. This measure of length was used because it could be more accurately determined on live fish than the more usual standard length, and was less susceptible to alteration than total length measurement. At the end of three months, and monthly thereafter for six months, one fish from each group was sacrificed for histological study of thyroid, pituitary and gonads. The fish were killed by immersion in Bouin's solution. Serial sections at 7μ containing the pituitary and thyroid were stained with Masson's triple stain made up of ponceau-acid fuchsin and fast green. Serial sections through the body region containing gonads were cut at 10μ and were stained with Harris's hematoxylin and eosin. The epithelial cell heights of the thyroid follicles were measured by a modification of Rawson and Starr's method (1938), and the mean cell heights were compared for statistical significance using the standard formula for the derivation of the value of $d/\sigma d$.



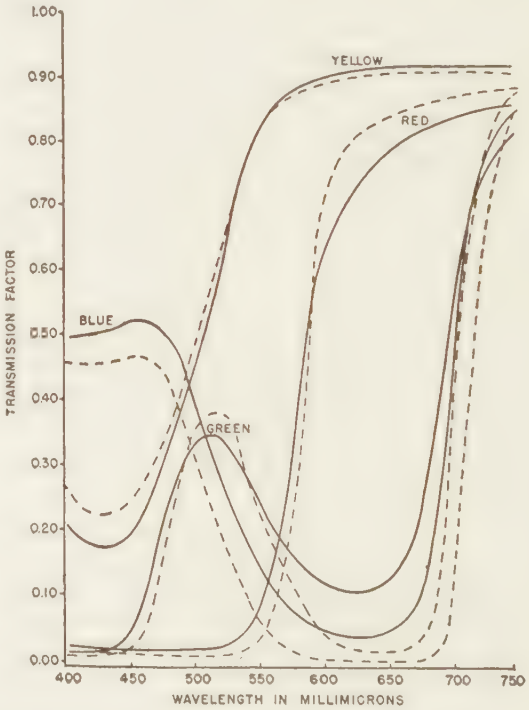
TEXT-FIG. 1. Spectrograms of colored filters obtained with a quartz spectrograph and a carbon arc lamp. Numbers 1, 2 and 7 represent the transmission of the carbon arc lamp alone; 3, 4, 5 and 6 represent respectively the transmission of the red, yellow, green and blue filters.

The luminous transmission of the colored filters, in foot candles, at the bottom of each tank, when empty, under average daylight conditions, was determined with a Norwood Director exposure meter, Model B, number 261, American Bolex Company. These values were respectively: control, 510; red, 135; yellow, 490; green, 100; blue, 110.

The spectral transmission by the colored filters was determined by means of a quartz spectrograph, with a carbon arc lamp as a light source. Although the carbon arc spectrum extends to include some of the ultraviolet, the transmission of these shorter wave lengths by the colored filters was of no concern because these wave lengths were blocked by the window glass skylight as well as by the sides and top of the aquaria. The spectrograms in Text-fig. 1 indicate that all of the filters except the red transmitted some of both the longer and the shorter wave lengths of visible light.

A more detailed analysis of the wave lengths transmitted by the colored filters was obtained from spectrophotometric tests on samples of the cellophane both before and after use, since it was possible that considerable fading could have occurred. These tests were carried out at the Electrical Testing Laboratories, New York City, with a Hardy Recording Spectrophotometer. The two series of transmittance curves are incorporated into Text-fig. 2. It is seen that the differences in transmission between the used and unused samples were small at most wave lengths. The yellow filter transmitted the most light, followed by the red filter, but the blue and green filters transmitted considerably reduced amounts of light. At the shorter wave lengths of 400 to 550 millimicrons, which included violet, blue and most of the green regions, transmission by the red filter was low enough to be considered insignificant. Although the green and blue filters transmitted only small amounts of the yellow and orange wave lengths, they transmitted about 80 percent. of the far red region of the spectrum.

From the energy distribution in the spectrum of a standard illuminant (C), which is an approximation of average daylight established by the International Commission for Illumination (Judd, 1933), it was seen that the energy content at 450-550 millimicrons exceeded that of all other spectral regions. This is the region blocked by the red filter, so that although more light was transmitted, radiant energy under this filter was probably no greater than under the blue and



TEXT-FIG. 2. Transmittance curves of the cellophane filters obtained from spectrophotometric tests with a Hardy spectrophotometer. The broken lines represent the transmission by the unused filters at the start of the experiment, and the solid lines represent the transmission by the used filters at the end of the experiment.

TABLE 1. MONTHLY MEAN LENGTH AND DEPTH IN MILLIMETERS OF FISH UNDER COLORED FILTERS

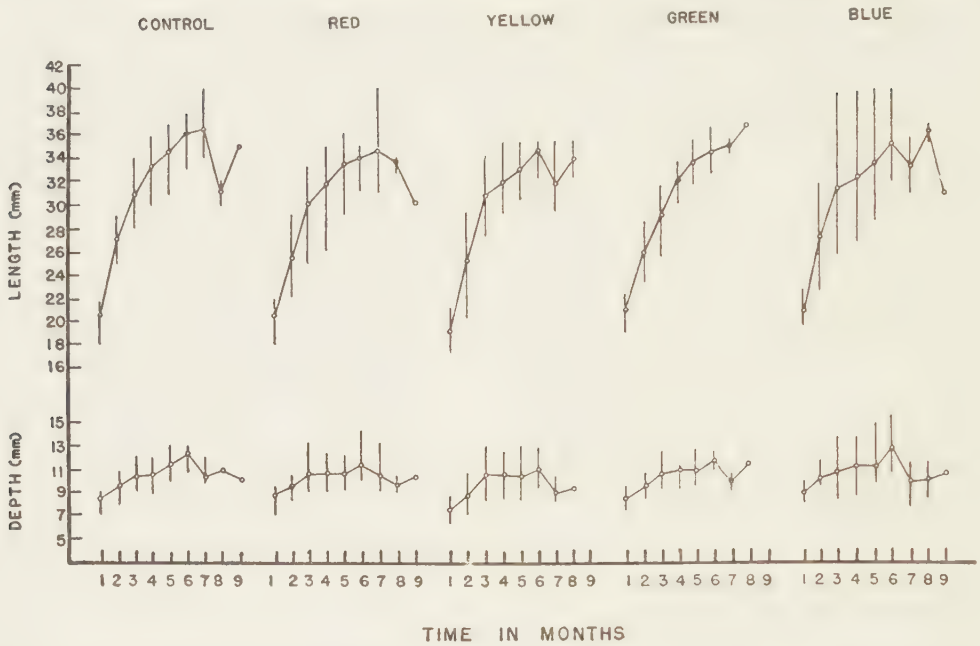
Filter	Number of Fish	Age in Months	Mean Length	Standard Error	Mean Depth	Standard Error
Control	6	2	20.7	.653	8.3	.304
	6	3	27.0	.527	9.5	.392
	6	4	30.8	.843	10.5	.391
	6	5	33.2	.843	10.8	.487
	5	6	34.4	.828	11.4	.455
	4	7	36.0	1.060	12.2	.416
	3	8	36.3	1.502	10.2	.606
	2	9	31.0	....*	11.0	...
	1	10	35.0	....	10.0	...
Red	6	2	20.7	.561	8.5	.312
	6	3	24.3	1.326	9.2	.367
	6	4	30.0	1.027	10.8	.548
	6	5	31.4	1.194	10.7	.451
	5	6	33.2	1.244	10.6	.455
	4	7	34.0	1.658	11.2	.829
	3	8	34.6	2.231	10.1	1.097
	2	9	33.5	....	9.5	....
	1	9½	30.0	....	10.0	....
Yellow	6	2	19.0	.472	7.3	.304
	6	3	25.0	1.312	8.7	.509
	6	4	30.7	1.018	10.5	.565
	6	5	31.5	.874	10.3	.561
	5	6	32.8	.912	10.0	.565
	4	7	34.0	.612	10.7	.650
	3	8	31.3	1.658	8.6	.545
	1	8½	35.0	....	9.0	...
	1	9	32.0	....	9.0	...
Green	6	2	20.5	.514	8.0	.236
	6	3	25.3	.765	9.0	.333
	5	4	28.4	1.252	10.2	.438
	5	5	31.6	.456	10.2	.334
	4	6	33.0	.707	10.5	.500
	3	7	34.0	.943	11.3	.236
	2	8	34.5	....	9.5	...
	1	9	36.0	....	11.0	...
Blue	6	2	20.7	.452	8.3	.193
	6	3	26.7	1.240	9.7	.304
	6	4	30.8	1.906	10.0	.707
	6	5	31.5	1.594	10.5	.612
	5	6	32.8	1.682	10.6	.799
	4	7	34.5	1.479	12.0	.935
	3	8	32.3	2.054	9.3	.981
	2	9	35.5	....	9.5	...
	1	9½	30.0	....	10.0	...

* Standard errors not calculated when less than three fish left in group.

green filters, whereas radiant energy under the yellow filter was considerably greater, although still inferior to the controls.

RESULTS

General behavior. — No behavior derangements could be attributed to the colored filters. As far as could be determined, feeding was normal and regular in all of the groups. *Astyanax mexicanus* is known to exhibit frequent "nervous" behavior patterns. In the course of one or several days these fish sometimes alternate



TEXT-FIG. 3. Monthly mean lengths and depths of the fish are indicated by small circles. Monthly extreme values of length and depth are indicated by vertical lines.

from a relatively quiescent state to an extremely active hostile condition, which occasionally results in a group annihilation (Breder, 1943).

Survival.—There were no differences in the ability to survive under the colored filters. During the course of the experiment one fish from each group except the control died from unknown causes. It appeared, however, that death was not caused by the experimental environments.

Growth.—The filtered light did not inhibit the body growth of the fishes, as seen from the data in Table 1, where the monthly mean lengths and depths and their standard errors are listed. The growth curves (Text-fig. 3), prepared from the mean lengths and depths plotted against time, have similar slopes, except in the last few months of the experiment. The fluctuations seen at this time were caused by a reduced number of fish as they were killed for histological study. Comparisons of the monthly size ranges of the fish, represented by the vertical lines in Text-fig. 3, indicate that the most extreme size differences were shown by the fish under the red and blue filters.

The greatest percentage of growth in mean length and depth at the end of five months occurred in the group under the yellow filter, and in the controls, whereas under the red filter this value was smallest. From the percentage growth at monthly intervals it was found that growth during the first month under the red filter was small, but by the end of the second month increased to the greatest value found in any of the other groups (Table 2). This probably reflects a slower adjustment to the red filter. Statistical examination of the data in this table indicates that these growth differences were not statistically significant.

Thyroid.—In the thyroid glands of *Astyanax* under one year old, maintained under normal laboratory conditions, the follicular epithelium varies from squamous to low cuboidal, and occasionally high cuboidal. The location of the follicles, which are diffusely scattered as in most other teleosts, and their normal histological structure, were described by Rasquin (1949).

No extreme deviations in thyroid histology were produced by the colored filters. Monthly variations in the height (Table 3) and activity of the follicular epithelial cells and differences in the amount and staining reaction of the colloid were seen in all of the groups. The thyroid hyperplasia observed by Rasquin (1949) in *Astyanax* maintained in complete darkness was not produced in these fish.

Small differences in thyroid activity revealed by careful analysis of the data are of sufficient interest to be further examined. It can be seen from the graphic representation of the mean

TABLE 2. PERCENTAGE INCREASE IN MEAN LENGTH AND DEPTH AT MONTHLY INTERVALS AND AFTER A FIVE-MONTH INTERVAL

Months	Number of Fish	Percentage Increase Under Colored Filters				
		Control	Red	Yellow	Green	Blue
			Mean Length			
1 -	6	41.2	27.1	40.0	35.6	43.5
2 -	6	24.8	42.9	38.0	23.0*	29.7
3 -	6	15.7	10.5	5.3	23.7	5.1
4 -	5	7.8	13.5	8.7	10.4	9.4
5 -	4	10.5	6.0	8.0	7.4	12.3
1-5	—	73.9	64.3	78.9	65.9	67.5
			Mean Depth			
1 -	6	30.8	24.1	38.9	30.3	37.8
2 -	6	25.6	55.2	46.2	36.4*	8.1
3 -	6	7.7	decr.	decr.	00.0	13.5
4 -	5	15.4	decr.	decr.	9.1	2.7
5 -	4	20.5	20.7	17.9	24.2	37.8
1-5	—	47.0	31.8	46.6	41.3	44.6

* Average of five fish.

thyroid epithelial cell heights (Text-fig. 4) that the control group showed the smallest variations in height, whereas all of the colored filters produced more atypical curves when compared with the controls, especially the blue and yellow filters. The values for the difference between the extremes of the mean thyroid epithelial cell heights were respectively: blue, 1.01; yellow, .70; red, .59; green, .56; control, .29 (all in microns).

Over 50 percent. of these variations in the mean thyroid cell height associated with the colored filters were found to be statistically significant, as seen in the lower part of Table 3. The mean cell heights were significantly decreased by the yellow filter, increased by the green and red filters, and both decreased and increased, in different fishes, by the blue filter.

Other changes in thyroid histology accompanied the variations in cell height. When cell height was high, the follicles were small, the epithelial cells contained vacuolated cytoplasm, and the stored colloid which had decreased in amount and changed in staining reaction, contained chromophobic vacuoles. When cell height was low, the follicles were enlarged and were filled with deeply staining dense colloid.

Pituitary.—The examination of serial sections revealed no changes in the histology of this gland that could be referred to the colored filters. The relative proportions and the size, distribution, cytoplasmic granulation and staining reactions of the acidophiles, basophiles and chromophobes of the transitional lobe—normally associated with cyclic changes in secretory activity—corresponded to the description given by Rasquin (1949) for the normal six- to twelve-month-old *Astyanax* pituitary. Vacuolated basophiles, normally found in this lobe, were more numerous in the five- to eight-month-old fish grown under the blue, green and yellow filters, than in the controls of the same age, whereas in all of the nine-month-old fish many vacuolated basophiles were present.

Ovary.—Fully mature yolk-filled ova were found in nine of the thirteen ovaries examined. Under each colored filter, however, there was one fish with only a few mature eggs. The data were insufficient to evaluate this finding because under similar normal conditions it is known that some fish mature earlier and develop faster than others. Some resorbing eggs, probably caused by a failure to ovulate, were found in all ovaries. This resorption process was best observed in the extremely large, fully mature ovaries from the seven-month-old control fish, and the six-month-old fish under the yellow filter. In the middle and posterior regions of these ovaries, all of the mature eggs appeared to be breaking down. They had become confluent into one large mass which contained eosinophilic yolk, fat-like vacuoles, reticular-like tissue, cho-

TABLE 3. INDIVIDUAL AND GROUP MEAN THYROID EPITHELIAL CELL HEIGHTS IN MICRONS OF FISHES UNDER COLORED FILTERS

Filter	Age in Months	Sex	Size in mm. Length by Depth	Mean Cell Height	Standard Error	Group Mean Cell Height	Standard Error
Control	5	M	34x11	2.585	.0368		
	6	F	34x11	2.725	.0356		
	7	F	38x13	2.510	.0399	2.55	.0444
	8	F	40x12	2.500	.0400		
	9	F	32x11	2.435	.0358		
Red	5	F	32x10	2.600	.0339		
	6	M	34x11	3.010	.0464		
	7	M	35x10	2.663	.0429	2.65	.2761
	8	F	40x13	2.420	.0417		
	9	M	34x9	2.575	.0378		
Yellow	5	F	35x12	2.670	.0443		
	6	F	33x11	2.625	.0335		
	7	F	35x12	2.300	.0367	2.36	.3623
	8	M	35x10	1.970	.0468		
	9	M	32x9	2.280	.0285		
Green	5	M	31x9	2.800	.0452		
	6	F	31x11	2.935	.0375		
	7	F	36x12	2.380	.0395	2.62	.3052
	8	M	34x9	2.425	.0389		
	9	M	36x11	2.545	.0368		
Blue	5	M	30x10	3.255	.0631		
	6	F	34x11	2.655	.0379		
	7	M	39x15	2.250	.0391	2.70	.1536
	8	M	35x11	2.470	.0528		
	9	F	35x11	2.855	.0334		

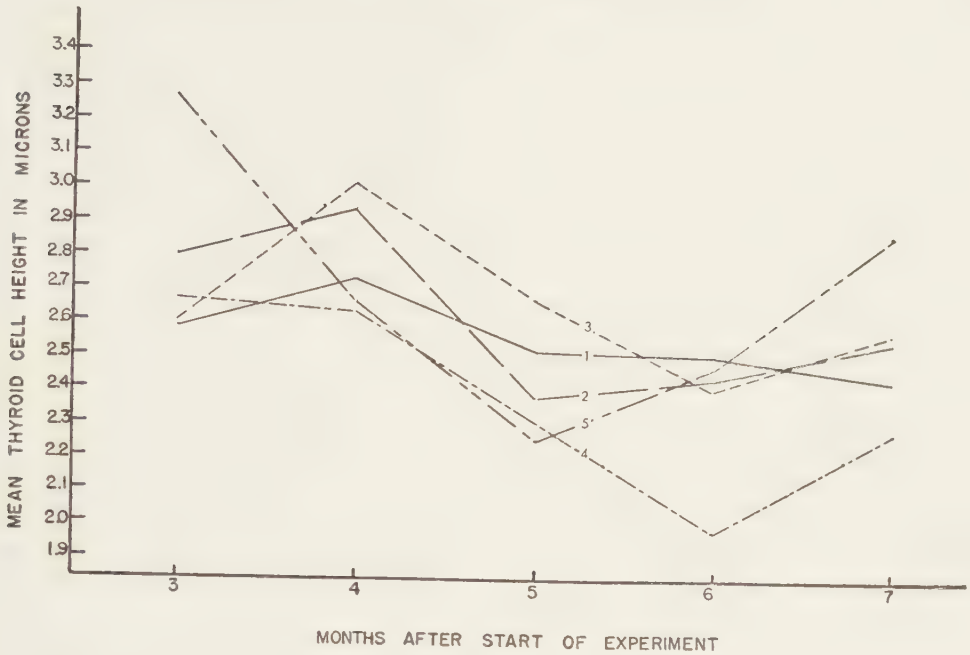
Comparisons made for statistical significance of individual mean thyroid cell heights

Fishes Compared	Significance
5 mos. control with 5 mos. green	3.6
5 mos. control with 5 mos. blue	9.2
6 mos. control with 6 mos. red	4.9
6 mos. control with 6 mos. green	4.1
7 mos. control with 7 mos. red	2.5 prob. sig.
7 mos. control with 7 mos. yellow	3.8
7 mos. control with 7 mos. blue	4.6
8 mos. control with 8 mos. yellow	8.6
9 mos. control with 9 mos. red	2.7
9 mos. control with 9 mos. yellow	3.5
9 mos. control with 9 mos. blue	8.5

rionic membrane remains and hyperplastic follicular epithelium.

In three of the four fish with ovaries that contained few mature eggs, many ova were resorbing prematurely. It is of interest that these fish were seven to nine months old (from the groups under the blue, green and yellow filters). In the five-month-old fish from the group under the red filter that was not yet fully mature, resorbing eggs were not found.

Testis.—The testis is organized into lobules which contain cysts of spermatogenic cells. As the cells mature they are shed into the lobular cavities where they are stored prior to passage into the sperm duct. Rasquin & Hafter (1951) described the normal structure of the testicular



TEXT-FIG. 4. Mean thyroid epithelial cell heights, from three to seven months after the start of the experiment, for all of the fish. Numbers 1, 2, 3, 4 and 5 represent respectively the controls and the groups under the green, red, yellow and blue filters.

lobules and Rasquin (1951) demonstrated the presence of osmicated granules in the sperm duct epithelium which are indicative of a probable secretory function.

Only one of the twelve males examined was from the control group. This made difficult the determination of specific effects of the filtered light. It was observed, however, from comparisons of serial sections through corresponding regions, that all of the testes contained mature sperm in the lumina of the lobules and in the sperm duct.

In five of the seven- to nine-month-old fish from the experimental groups (two from yellow, one each from the red, green and blue groups) the testes contained very little spermatogenic tissue. This was also observed in some of a series of control males of approximately the same age, examined for another experiment, which indicates that this lack was probably not caused by the filtered light.

Discussion

The reduction of luminous intensity and radiant energy by the red, green and blue filters, compared with the controls, could account for the decreased total growth and increased thyroid activity observed in these groups. Similar but vastly greater changes were found when *Astyanax* were maintained in total darkness (Rasquin, 1949). Yung (1881) reported a spectral effect on the growth rate of salmon and tadpoles, but he used filters that differed in the transmission of radiant energy. Rugh (1935) analyzed the properties of the filters used by Yung and found that the transmission of the most radiant energy resulted in the fastest growth. Rugh also found, in his own experiments, that when radiant energy was equalized, differences in wave length and luminous intensity produced no differential effects on the growth rate of tadpoles. This relationship between radiant energy and growth rate was also found in these experiments on *Astyanax*. The red filter transmitted more light than the blue and green filters, but about the same amount of radiant energy. The percentage increase in length was approximately the same under all three filters. The absence of most of the shorter wave lengths under the red filter may also have contributed to the small length increase. The presence of both the shorter and longer wave lengths of visible light were found to be essential for the normal growth of young chicks (Sheard & Higgins, 1928; Sheard, Higgins & Foster, 1930). Constant housing of these chicks behind an amber glass filter that transmitted only the longer visible wave lengths of sunlight retarded growth and development.

Crawford (1930) noted that blue light resulted in the slowest rate of growth of young salmon, and also the heaviest mortality; red light produced growth effects similar to those produced by total darkness; and green and yellow light were optimal for growth. He did not publish any data, however, on the properties of the filters he used. Red and blue light were found to accelerate the growth of young rats (Ludwig & von Ries, 1931), but this was not confirmed by Allardyce, et al. (1942), who found no consistent differences in growth rate following maintenance under colored, colorless and black filters.

The variability in the growth of young fishes often encountered under normal conditions may be partially responsible for the small differences observed in the groups under the colored filters. Consideration should also be given to the difference in sex distribution in the different groups, since the fish were sexually immature at the start of the experiment. In *Astyanax,* females usually attain a larger size than males, so that the predominance of females in the control and yellow groups may therefore, in part, explain the greater total growth that occurred in these groups.

Modlinger (1941) found that red light and darkness increased the epithelial cell height and decreased the iodine content of the colloid of the dove thyroid, and these changes coincided with those that took place during the annual cycle. Pighini (1941) also reported that monochromatic red, yellow, green and blue light all produced increased thyroid activity in guinea pigs. The effects were not wave-length specific, and may have been caused by the decreased light and radiant energy transmitted by the colored lights. In *Astyanax,* the yellow filter significantly decreased thyroid cell height, and this appeared to be a wave-length effect, since the light and radiant energy transmitted did not differ substantially from the control. The blue filter significantly increased thyroid cell height in two fish, but significantly decreased cell height in another fish. The increased cell height was explained by a decreased transmission of light and radiant energy, but it is impossible to explain the opposite effect without additional data. It is possible that these results, although statistically significant, are not biologically significant because of the nature of the material.

Other studies also indicated that decreased light or darkness results in increased thyroid activity (Bergfeld, 1931, in rats; Puntriano & Meites, 1951, in mice; and Rasquin, 1949, in the teleost, *Ameiurus nebulosus*), although Mayerson & Branch, 1934; Mayerson, 1935; and Kenyon, 1935, in rats; and Stein & Carpenter, 1943, in the salamander, *Triturus viridescens,* did not confirm this response.

That all of the colored filters altered the thyroid activity of *Astyanax* indicates the role of this gland in the general response to a changed environment. An altered metabolic rate may have been involved in this response, although it is not definitely known that the teleost thyroid gland is a regulator of metabolism (Etkin, Root & Mofshin, 1940, and Matthews & Smith, 1947). Some indication of the thyroid's metabolic function is seen by the reports that total darkness increased both the oxygen consumption (Schlagel & Breder, 1947) and the thyroid activity (Rasquin, 1949) of *Astyanax.*

Although no prominent changes in the pituitary of *Astyanax* were produced by the colored filters, Pighini (1941) found that red, yellow, green and blue light all produced the early appearance of acidophiles in the anterior lobes of young guinea pigs. This was attributed more to the lower luminous intensity and radiant energy transmitted by the colored lights than to specific wave-length effects. In addition, darkness reduced the relative number and activity of pituitary basophiles in *Astyanax* (Rasquin, 1949) and in frogs (Florentin & Stutinski, 1936; Stutinski, 1936; and Woitkewitsch, 1944).

The many resorbing ova found in all of the ovaries of *Astyanax* did not appear to be effects of specific wave lengths. The breakdown of mature ova, in the absence of spawning, and their subsequent resorption, has been described as a normal occurrence in other teleost ovaries (Brock, 1878; Barfurth, 1886; Cunningham, 1897; and Wallace, 1904). These degenerating ova undergo fatty changes, accompanied by the immigration of much cell debris into the substance of the egg. It is still uncertain whether this cell debris comes from a growth and proliferation of the follicular epithelium (as in trout ova, Barfurth; and in *Zoarces viviparus,* Wallace), from a proliferation of the cells from the connective tissue in the wall of the follicle (as in *Trigla hirunda,* Cunningham), or from both of these locations (as in the bitterling, *Rhodeus amarus,* Bretschneider & de Wit, 1941).

It has been demonstrated by the present work that despite all of the spectral, light intensity and radiant energy reductions provided by the colored filters, the fish were able to maintain the essential integrity of their endocrine systems. Evidently, for this stability, the presence of some visible radiation as such is of greater significance than the exact spectral quality of that radiation, for which there are many corroborating studies

in the literature. There is need for further experiments which will utilize filters of more refined properties and which will operate at intensities between those used in the present study and the zero intensity used by Rasquin (1949). The minimal light intensity that will support normal endocrine structure and function, as well as the possible importance of specific wave lengths at such a lowered intensity of light, are problems yet to be studied.

Summary and Conclusions

1. Two-month-old *Astyanax mexicanus* were grown under daylight filtered by red, yellow, green and blue cellophane sheets, for three to eight months, after which the histology of the thyroid, pituitary and gonads was compared with that of controls maintained without any filter. The cellophane sheets were analyzed for the transmission of the spectrum and for luminous intensity.

2. At the end of five months, the fish under the yellow filter showed about the same percentage of increase of growth in body length and depth as the controls. A smaller percentage of increase was attained under the red, green and blue filters, because of the decreased light transmitted, but these lower figures were not significantly different from the controls.

3. Thyroid activity in some of the fish under the red, green and blue filters was significantly increased over the controls, and was probably produced by the decreased transmission of these filters. Some spectral influence of the yellow filter was presumed to be responsible for the significantly decreased thyroid activity observed in some of these fish. Additional data are needed to explain the significantly decreased thyroid cell height in one fish grown under the blue filter. The biological significance, if any, of these alterations in thyroid activity is yet to be ascertained.

4. The structure of the transitional lobe of the pituitary and the testes showed no significant changes induced by the colored filters.

5. Some ovaries that were not fully mature were found in fish raised under the colored filters, with prematurely resorbing ova, especially under the yellow, green and blue filters. The significance of this item is unknown.

6. It was demonstrated that despite all of the spectral, light intensity and radiant energy reductions provided by the colored filters, the fish were able to maintain the essential integrity of their endocrine systems.

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4

Fungus Associated with a Granuloma in a Turkish Fish, *Aphanius chantrei* Gaillard

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(Plates I & II; Text-figures 1-11)

INTRODUCTION

RELATIVELY few fungus infections that produce tumors in fishes have been studied in detail. Montpellier & Dieugeide (1933) briefly described a "pseudo-tumeur mycélienne" in a North African *Cyprinodon fasciatus,* and recently Walker (1951) reported a case in *Salmo* sp. The present paper describes a granuloma caused by an undetermined fungus in *Aphanius chantrei,* a small, freshwater cyprinodont fish indigenous to Turkey.

Since the blood cells play an important role in the development of granulomas, it is fortunate that the papers by Duthie (1939) and Catton (1951) on fish blood elements are now available. This makes possible a more complete analysis of the piscine granuloma than has previously been presented.

The present study may have special significance in view of the recent investigations of Diller & Fisher (1950), who demonstrated the presence of inter- and intracellular fungal structure including mycelia (Fungi Imperfecti related to Blastomycetes) from transplanted, induced and spontaneous tumors of the mouse and of man.

MATERIALS AND METHODS

A number of *Aphanius chantrei* were collected near Samsun, a town in northern Anatolia on the Black Sea. They were kept for about a year in the aquarium of the Zoological Institute of the University of Istanbul at Baltalimani on the Bosporus. One of these specimens, a female 45 mm. in standard length, developed a tumor on the dorsal surface over the operculum and pectoral fins (Pl. I, Fig. 1). The swelling did not interfere with the normal behavior of the fish.

The fish was fixed in a mixture of 76 parts of saturated aqueous mercuric chloride, 20 parts of formalin and 4 parts of glacial acetic acid. The anterior half of the animal was decalcified in nitric acid, dehydrated in alcohol, cleared in xylol, embedded in paraffin and cross-sectioned at 10 μ. Sections were stained either with Mayer's hematoxylin (hemalum) and eosin, Heidenhain's iron hematoxylin and eosin, Mallory's azan stain or van Gieson's collagen stain, or by Gram's method.

GROSS DESCRIPTION OF THE TUMOR

The swelling was smooth, soft, and projected dorsad from the right side of the body (Pl. I, Figs. 1-3; Text-figs. 1, 2). It measured 7 mm. in length, 5.5 mm. in depth and 4 mm. in height. The entire mass was covered by a layer of skin and was the same color as the body of the fish. The scales over the swelling were separated and no longer imbricated. Scales were missing on the right dorsal surface and in some other areas (Text-figs. 1, 2).

Examination of the sections showed that the growth was located in the dorsal musculature extending from the region just back of the head (Pl. I, Figs. 1, 2) to that near the gonads.

In some regions the skin in contact with the tumor was hyperplastic (Pl. I, Fig. 3; Text-fig. 1). In other regions the skin was normal and there was a space between the boundary of the tumor and the dermis.

At the most anterior portion of the growth there was no external swelling but the skin was hyperplastic and the scale pockets were larger

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TEXT-FIG. 1. A cross-section of the granuloma over the gill region. The new growth arises cone-like above the dorsal surface of the body. Note the hyperplastic epidermis on the right and the nodules in the granuloma. **Ep** = epidermis, **Gr** = granuloma, **I.t.** = infiltrating tissue, **M** = musculature, **Me** = melanophore, **Sc** = scale. Hemalum-eosin.

than those over the unaffected regions of the body. Here the growth, which contained some melanophores, had infiltrated the muscles between the skin and the skull.

A little further caudad the growth enlarged and extended above the body surface. The center of the growth contained nodule-like formations. On the right side of the mass, the epidermis and dermis of the skin were hyperplastic and extended into the growth. The scales and the scale pockets were wanting (Text-fig. 1). The left side was normal.

Still further caudad, in the gill region, the growth was larger and rounder. The overlying skin was thin and contained scales. The growth had infiltrated the dorsal trunk musculature of the right side of the body. Here the growth was composed primarily of whorl-like nodules which were surrounded by a fibrillar, capsule-like tissue.

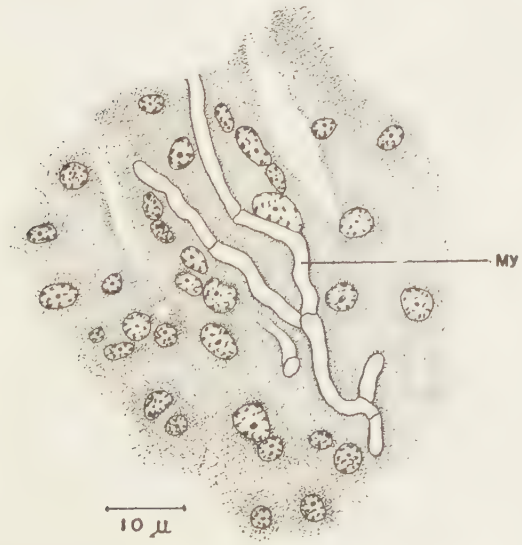
The largest part of the growth developed in the region above the liver (Text-fig. 2). The entire mass was round and was composed of two large and four small foci, each of which was encapsulated. The centers of some of the foci were necrotic. At this level the infiltration of the muscles was seen only on the right side, but the pressure of the growth had forced the central muscle mass to the left. Posterior to this region, the tumor as a whole was smaller. Microscopic examination of the region just beyond the externally visible tumor revealed granulation tissue cells.

HISTOLOGICAL AND CYTOLOGICAL OBSERVATIONS

The granuloma is composed of a reticular connective tissue stroma and of proliferated lymph cells, leucocytes, mast cells, giant cells, fibroblasts and capillaries. No bacteria were found in sections stained by Gram's method.

The mycelia of an undetermined species of fungus are surrounded by lymphocytes, leucocytes and fibroblasts (Text-figs. 3-5). Most of the hyphae show septa and branches (Text-fig. 3; Pl. II, Fig. 4). The hyphae may be intracellular or intercellular. They lie either in granulation tissue as individual filaments or in an irregular network of mycelia (Text-figs. 3, 4). In hemalum-eosin-stained sections they were yellowish-pink in color; stained by Mallory's they are blue. All hyphae are Gram negative. They show a hyalin structure and homogeneous plasma. The width of the hyphae varies from 1.2 to 2.5 μ while their length varies approximately from 15 to 110 μ.

TEXT-FIG. 2. A cross-section in region of the liver showing different foci and necrotic area (**N.a.**) in the granuloma. **Ep** = epidermis, **Gr** = granuloma, **M** = musculature, **Me** = melanophore, **Sc** = scale. Hemalum-eosin.

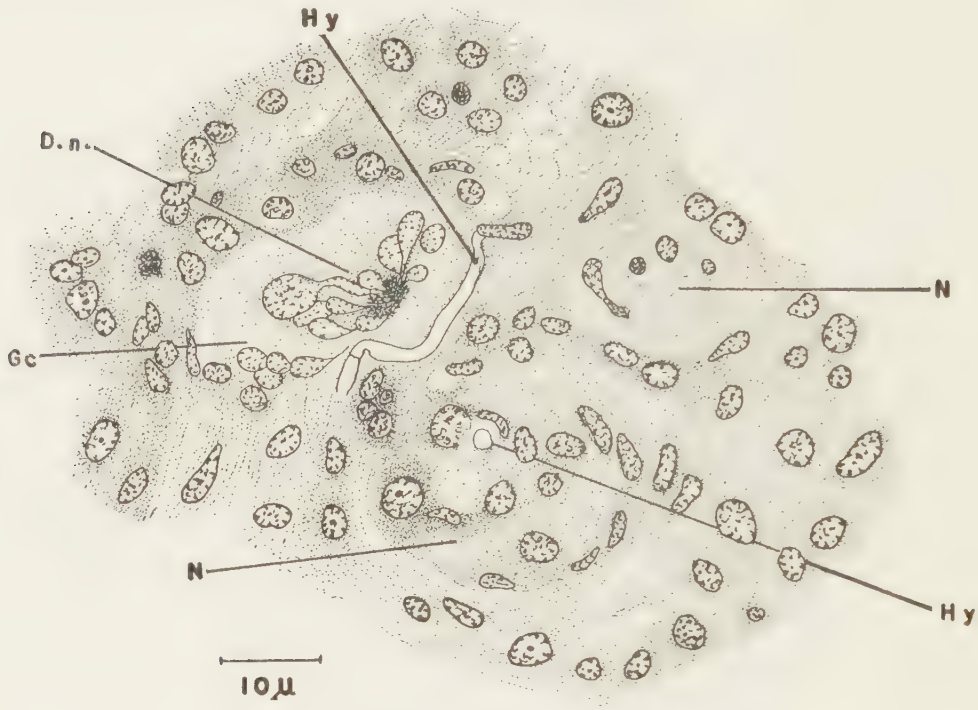


TEXT-FIG. 3. Part of a nodule containing a mycelium (**My.**). Note the septa in the hyphae. Hemalum-eosin.

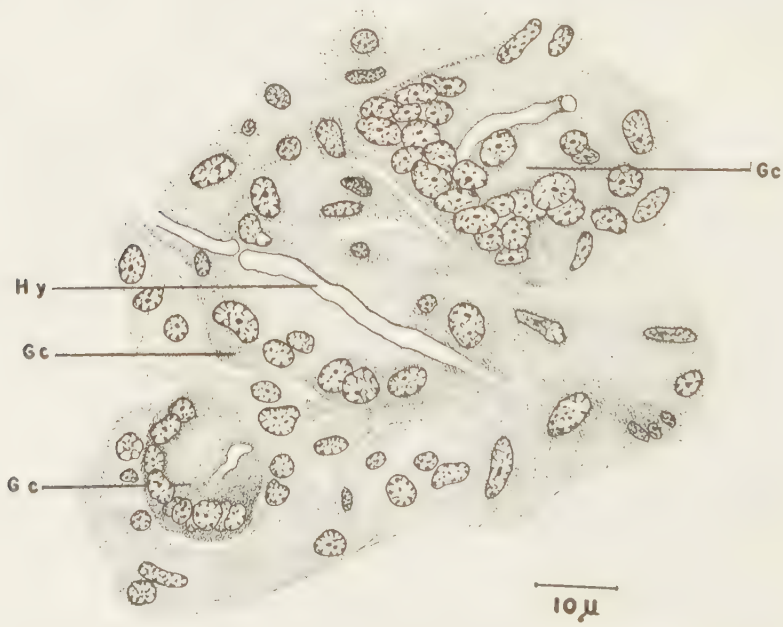
The fibers of the connective tissue stroma, in the center of the growth, are reticular and run approximately parallel around the whole granuloma (Text-figs. 6, 7). The mesenchyme cells or reticulum cells are 9 to 13 μ, spindle-shaped, and have elongated nuclei (3.5 to 13 μ) which contain granular chromatin. These cells are attached to the fibers.

Lymphocytes of different shapes and sizes, many of which show mitosis, are scattered between the reticular network. The majority of them are round, except those around the nodules which are elongate. These lymphocytes have a relatively thin plasma mass around their nuclei, which contain either granular chromatin or a chromatin network. They measure 6 to 9 μ. Their nuclei are 3.5 to 5.5 μ. These cells are characteristically found around mycelia (Text-figs. 6-8).

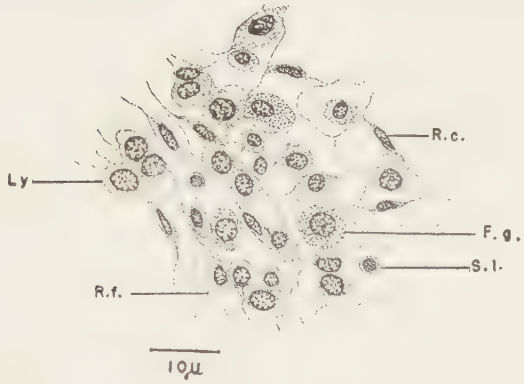
More finely granulated lymphocytes, called "fine granulocytes" by Duthie (1939) and Catton (1951), are found in the reticulum of the granuloma. These cells possess fine eosinophilic granules and measure 4.5 to 8.5 μ. Their nuclei, which measure 3 to 4.5 μ, contain a granular network in which the nucleoli can be seen in some instances. These fine granulocytes may be



TEXT-FIG. 4. Part of the granuloma showing a giant cell (G.c.) with dividing nuclei (D.n.). One of two small nodules (N) contains a hypha (Hy), seen in cross-section, and the other contains a degenerating cell. Hemalum-eosin.



TEXT-FIG. 5. Part of the granuloma showing three different giant cells (G.c.), each of which contains a hypha (Hy). Hemalum-eosin.



TEXT-FIG. 6. Reticular stroma of the granuloma showing reticular fibers (R.f.), reticulum cells (R.c.), lymphocytes (Ly), fine granulocytes (F.g.) and small lymphocytes (S.l.).

found either in capillaries or in the reticulum (Text-figs. 6-8). The fine granulocytes apparently pass through the blood vessels as shown in Text-fig. 8. Occasionally they may assume an elongated form, forming oval nuclei.

Some very small, round lymphocytes, having a diameter of 2.5 to 3.5 μ, are also seen, but rarely. These "small lymphocytes" have small amounts of cytoplasm around their nuclei. The nuclei, which are 1.5 to 2.5 μ in size, contain fine and extensive granular chromatin (Text-fig. 6, S.l.). These cells are similar to those called "lymphoid hemoblasts" by Duthie (1939) and "small lymphoid hemoblasts" by Catton (1951).

Another type of granuloma cell is represented by coarse granulocytes or mast cells. These are found mostly in the fibrillar, infiltrating, capsule-like zone around the granuloma (Text-fig. 9) and in the hyperplastic epidermis between the basal cells (Text-fig. 10). These mast cells or coarse granulocytes (10 to 20 μ) are spindle-shaped, round or oval and contain large eosinophilic granules. The nuclei are relatively small (2.5 to 3.5 μ). They are mostly eccentric and contain granular chromatin. These cells are found in the tissue of the new growth, but not in the blood vessels, nor are they found in the blood of a normal *Aphanius*.

The fibroblasts, which are elongated cells with oval or spindle-shaped nuclei, are scattered in the granuloma. They measure 13 to 23 μ and their nuclei, which very often contain a visible nucleolus, are 9.5 to 14.5 μ in size (Text-figs. 7-9). The fibroblasts take part in the infiltration of muscle and the formation of nodules in the granuloma.

Macrophages are found in necrotic areas. They are smaller than fibroblasts, similar to the lymphocytes and difficult to distinguish from the latter.

Giant cells are distributed in the granulation tissue, particularly where the mycelia cf fungus are scattered (Text-figs. 4, 5). They are polymorphic and contain round or oval nuclei which have nucleoli and loose chromatin nets. The nuclei are very often at the periphery of the cells and often form "pearls." The number of nuclei varies, many cells containing 10 to 27. The cells measure 19 to 40 μ and their nuclei, 3.2 to 8 μ. Text-fig. 5 shows three different types of giant cells embedded in granulation tissue, each of which has phagocytized one hypha.

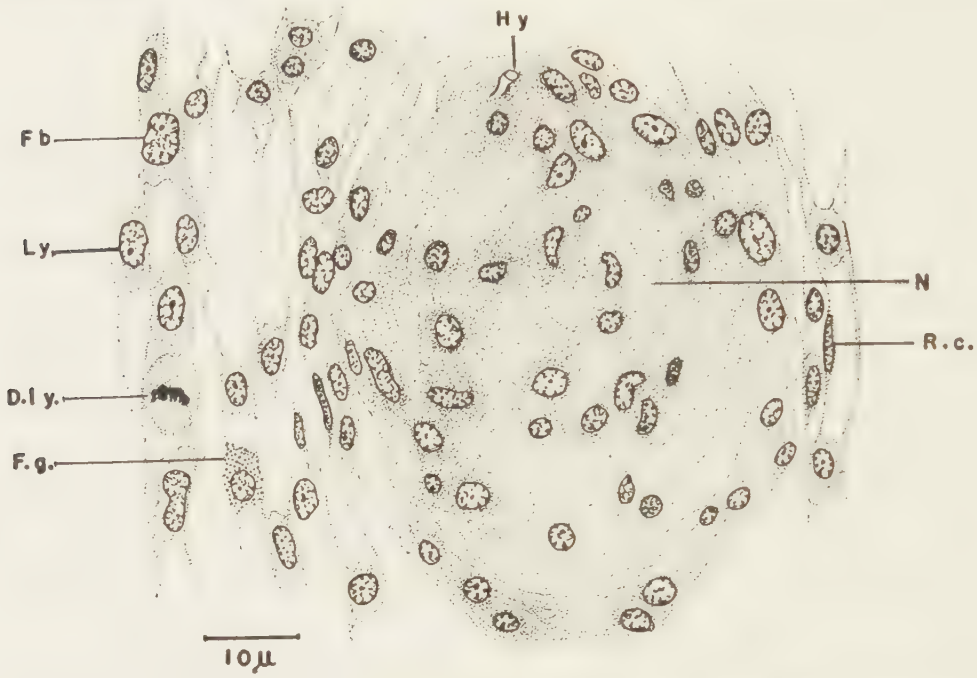
Whether giant cells are derived from fibroblasts or lymphocytes or endothelial cells has not been decided. Nuclear division was found in one of the giant cells. As shown in Text-fig. 4, the nuclear divisions are most peculiar. They probably represent a kind of amitotic division which may produce the pearl-like distribution of nuclei. Plehn (1906) found a similar type of nuclear division in a sarcoma in the trunk muscles of *Phoxinus laevis*. According to her, after such division multinuclear giant cells may appear. Some of the giant cells contain pyknotic nuclei.

The cells including lymphocytes and fibroblasts, which accumulate around the mycelia, form the nodules of granulation tissue (Pl. II, Figs. 5-6). In the formation of nodules lymphocytes are especially active (Text-figs. 7, 8). The nodules are round, vary in size, and are encapsulated by a reticular stroma, as shown in Text-fig. 7.

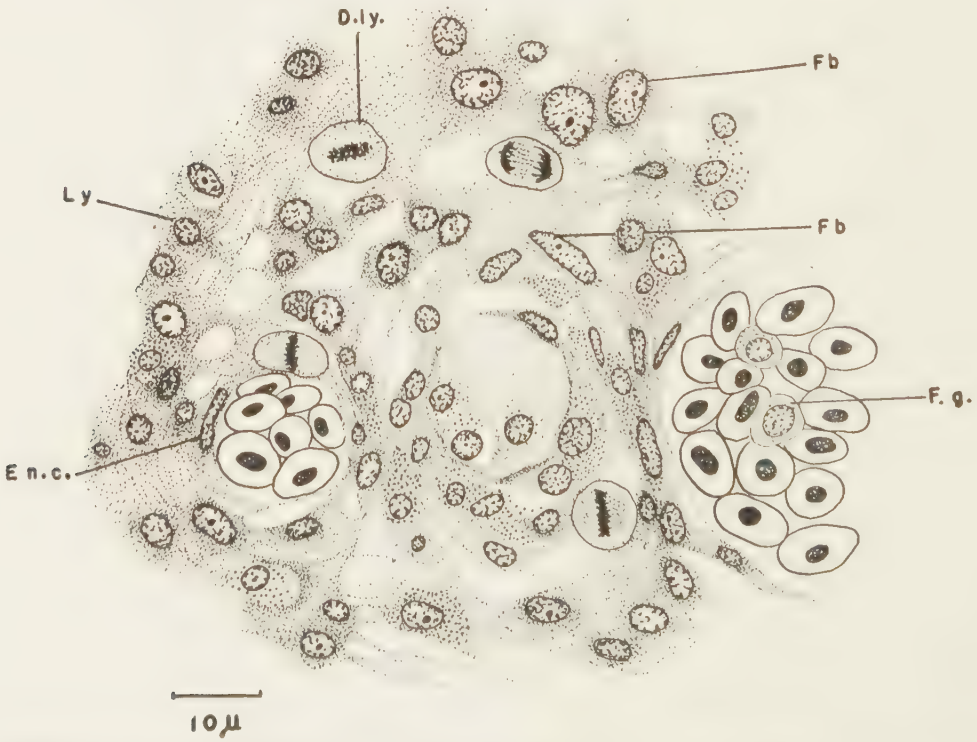
Some necrotic areas are found in the center of the granuloma. These areas contain cell debris, hyphae and macrophages (Pl. II, Fig. 5).

Capillaries are found either in or around the granuloma (Text.-fig. 8). They are hyperemic and their endothelial cells are sometimes hypertrophic. Some erythrocytes lie free in the granulation tissue.

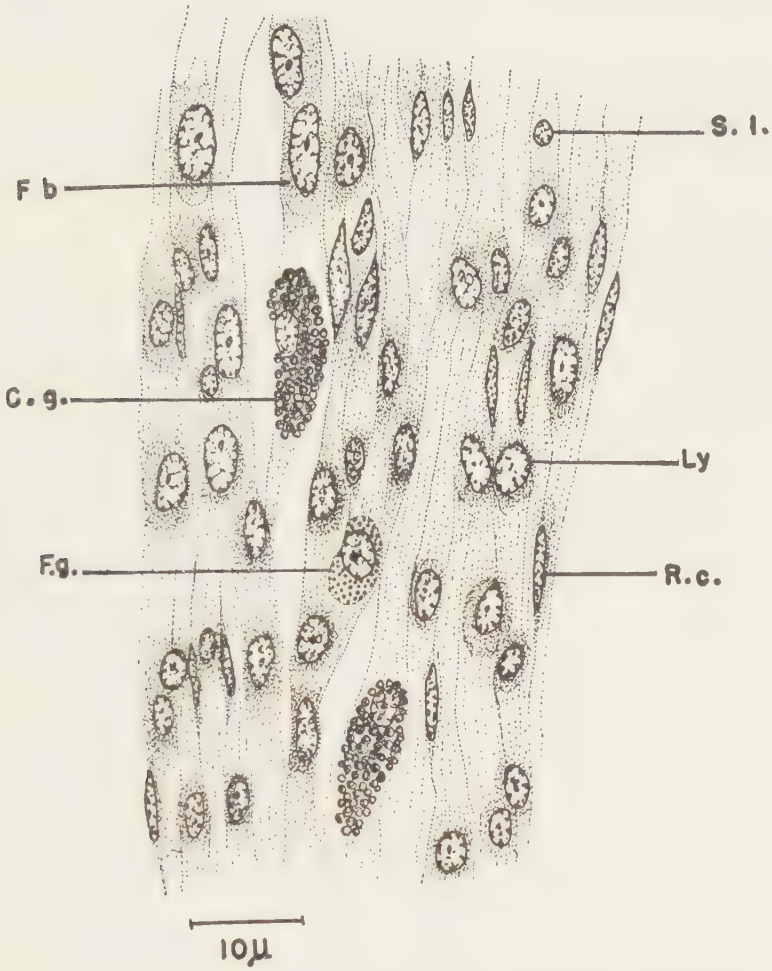
The epidermis over the granuloma is partly normal and partly hyperplastic. The normal epidermis of *Aphanius* is 20 to 30 μ thick and is composed of about six layers of squamous epithelium cells, oval or round mucous cells and basal cells, and some melanophores in the basal part of the epidermis. The hyperplastic epidermis over the granuloma is approximately 130 μ thick and has 20 to 25 cell layers (Text-fig. 10). Besides the squamous epithelial cells, mucous cells and basal cells, some coarse granulocytes are found in the proximal part of the hyperplastic epidermis. Since the coarse granulocytes in normal fish are only in connective tissue, they probably come from granulation



TEXT-FIG. 7. A nodule (N) in the granuloma, surrounded by fibrillar tissue. D.ly = dividing lymphocyte, F.g. = fine granulocyte, Fb = fibroblast, Hy = hypha, Ly = lymphocyte, R.c. = reticulum cell. Hemalum-eosin.



TEXT-FIG. 8. Part of the granulation tissue containing blood capillaries and dividing lymphocytes (D.ly). En.c. = endothelium cell, F.g. = fine granulocyte, Fb = fibroblasts, Ly = lymphocytes. Hemalum-eosin.



TEXT-FIG. 9. Part of the fibrillar tissue which surrounds the granuloma. **C.g.** = coarse granulocyte (mast cell), **F.g.** = fine granulocyte, **Fb** fibroblast, **Ly** = lymphocyte, **R.c.** = reticulum cell, **S.I.** = small lymphocyte. Hemalum-eosin.

tissue which in some regions is adjacent to the epidermis. The part lying between the squamous and basal cells of the hyperplastic epidermis is looser than in the normal epidermis. In some regions, the hyperplastic epidermis resembles granulation tissue in character and contains lymphocytes, fine granulocytes and hyphae of fungus besides epidermis cells. As the granuloma grew upwards, the overlying epidermis apparently became stretched. The epidermis thus grew parallel to the new growth.

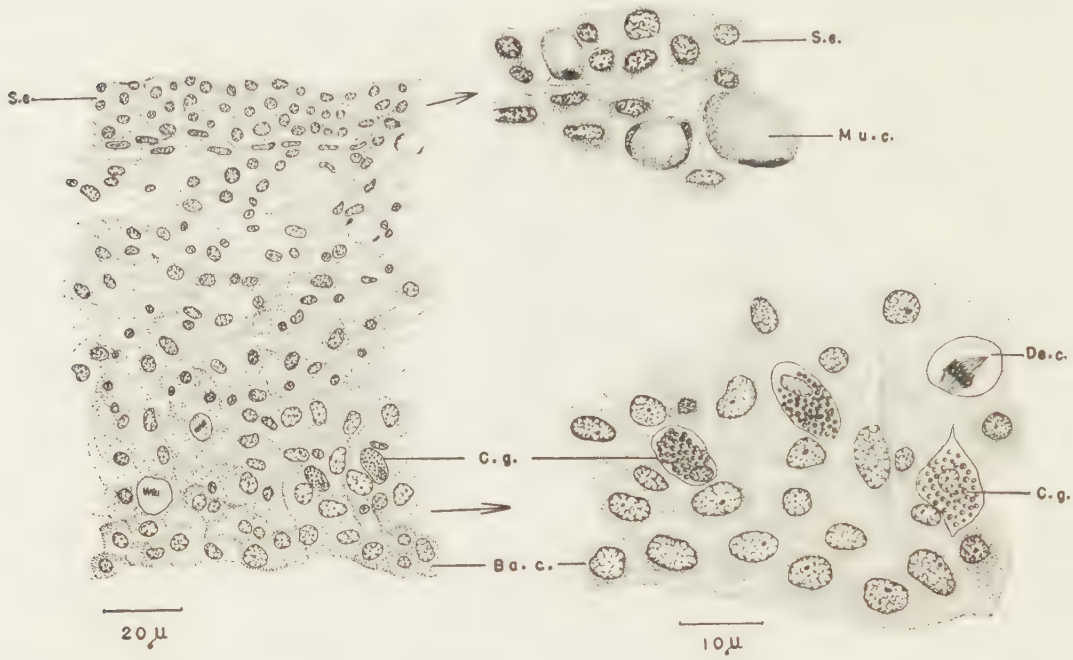
The scales are disarranged in some regions because of the epidermis growing under them, elevating them away from the dermis.

The fibrillar, capsule-like tissue which surrounds the granuloma infiltrates the subjacent musculature (Text-fig. 11; Pl. II, Fig. 7). At its deepest penetration, the invading granuloma cells appear fibrosarcoma-like and malignant.

DISCUSSION

In the granuloma described above, two phenomena must be distinguished. One is the cellular reaction of the body to the fungus infection. This results in the formation of granulation tissue in the infected area. Some of the cellular elements of granulation tissue, such as lymph cells, leucocytes and fibroblasts, form a nodule around either the mycelia or a single hyphae. The second phenomenon is the formation of a fibrosarcoma-like growth. The granulation tissue appears to lose its protective function and becomes a malignant growth. This tumor in *Aphanius* may be regarded as an "infective granuloma," as defined by Hamperl (1944) and Ogilvie (1947) in human pathology.

Human granulomas are essentially similar in cellular elements to those of fishes (Ash & Spitz, 1945; Ewing, 1940).



TEXT-FIG. 10. Hyperplastic epidermis overlying the granuloma. **Ba.c.** = basal cells, **C.g.** = coarse granulocyte, **De.c.** = dividing epithelial cell, **Mu.c.** = mucous cell, **S.e.** = squamous epithelium. Hemalum-eosin.

The species of infectious fungus could not be identified. As Ash & Spitz (1945) have pointed out, "It is usually not possible to identify a fungus in a histologic section. . . . The spores and mycelia of different species are too much alike to permit classification solely on morphology." Since the hyphae found in *Aphanius* contain septa, it can be said that this fungus does not belong to the Saprolegniaceae (Plehn, 1912).

The following reactions to the fungus were seen in *Aphanius*: a hyperplasia of lymph cells and leucocytes and the formation of giant cells. Similar general responses were found by Montpellier & Dieugeide (1933) in *Cyprinodon,* and by Walker (1951) in *Salmo.*

Some specific inflammatory responses and the formation of granulation tissue in fishes are mentioned by Plehn & Mulsow (1911), Takahashi (1929), Thomas (1931), Plehn (1938), Drew (1910-13), Wurmbach (1951), Breider & Schmidt (1951), etc., but the authors give few, if any cytological and histological details. Plehn (1910) and Schäperclaus (1941) report that in a disease called "Drehkrankheit," a sporozöon, *Lentospora cerebralis,* causes a granuloma in the auditory organs of trout, destroying this organ.

With regard to the origin of coarse granulocytes or mast cells, which are seen only rarely in the blood of fishes, several authors indicate that they come from the connective tissue. Michels (1923), studying a whitefish (*Leuciscus* sp.) and the carp (*Cyprinus carpio*), suggested this origin. Duthie (1939) and Catton (1951) have frequently observed these cells in connective tissue and rarely in the blood of a variety of teleost fishes. From my observations, the views of Michels seem valid.

SUMMARY

1. The histology and cytology of a granuloma associated with an undetermined fungus infection are described in a Turkish freshwater cyprinodont, *Aphanius chantrei.*

2. The granuloma mass, covered by a layer of skin, is found on the dorsal surface between the posterior margin of the operculum and the region of the pectoral fins.

3. The granuloma is composed of reticular connective tissue stroma and of proliferated lymph cells, leucocytes, mast calls, phagocytic giant cells, fibroblasts and macrophages. This mass is highly vascularized.

4. The mycelia of a fungus are scattered in the granulation tissue and are surrounded by lymphocytes and fibroblasts. These form definitive nodules in the granuloma.

5. The overlying epidermis, in some regions, is hyperplastic and shows partly the characteristics of granulation tissue.

TEXT-FIG. 11. Muscle infiltrating and fibrosarcoma-like tissue (I.t.). In.m. = infiltrated musculature, M = musculature. Hemalum-eosin.

6. The granuloma mass is surrounded by a fibrillar tissue which infiltrates the subjacent musculature. This infiltrating tissue is fibrosarcoma-like and appears to be malignant.

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EXPLANATION OF THE PLATES

(All photomicrographs were made from hemalum-eosin stained sections).

Plate I

Fig. 1. Granuloma on the dorsal surface in the region between the operculum and the pectoral fins of a female cyprinodont, *Aphanius chantrei*. About 1.4 ×.

Fig. 2. Cross-section through the gill and operculum region showing the granuloma as a round, cone-like mass arising over the dorsal surface. 8.5 ×.

Fig. 3. Another, more posterior, cross-section showing several foci of granuloma, one of which contains a large necrotic area. 8.5 ×.

Plate II

Fig. 4. Section showing two hyphae of a fungus in the granulation tissue. 1600 ×.

Fig. 5. Section through one part of the granuloma showing many nodules. A necrotic area (gray) may be seen in lower left portion. 65 ×.

Fig. 6. Section showing a part of the granuloma. Two large and some small nodules in the granulation tissue are shown at the lower right. Fibrillar and capsule-like tissue are at the lower left. These tissues are composed of fibroblasts, lymph cells and leucocytes, which infiltrate the musculature (extreme left). 375 ×.

Fig. 7. The muscle infiltrated by fibrillar, fibrosarcoma-like tissue. Some muscle is not yet completely destroyed.

FIG. 1.

FIG. 2.

FIG. 3.

FUNGUS ASSOCIATED WITH A GRANULOMA IN A TURKISH FISH, APHANIUS CHANTREI GAILLARD.

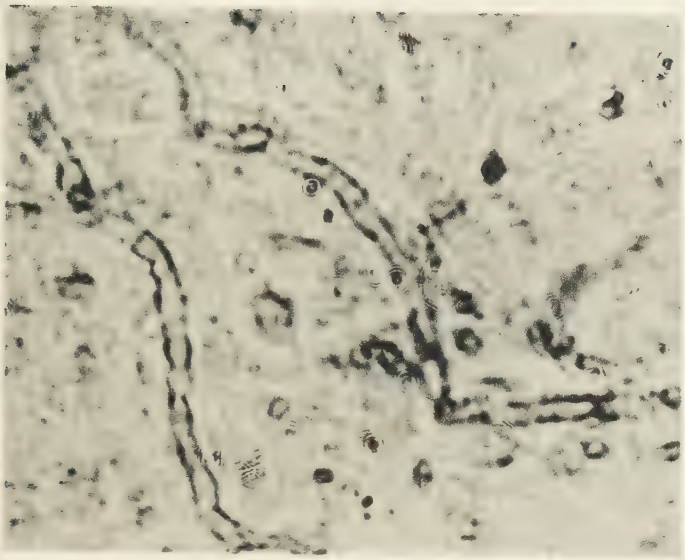

FIG. 4.

FIG. 5.

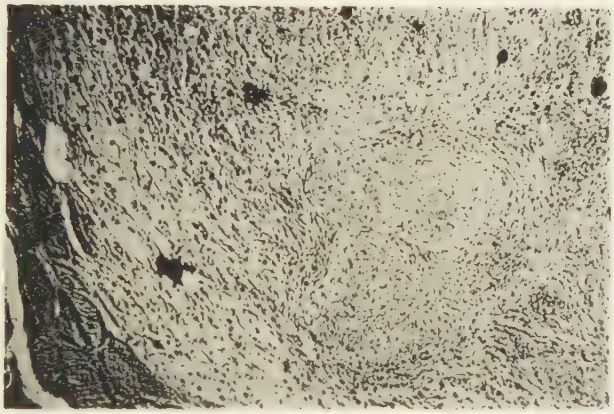

FIG. 6.

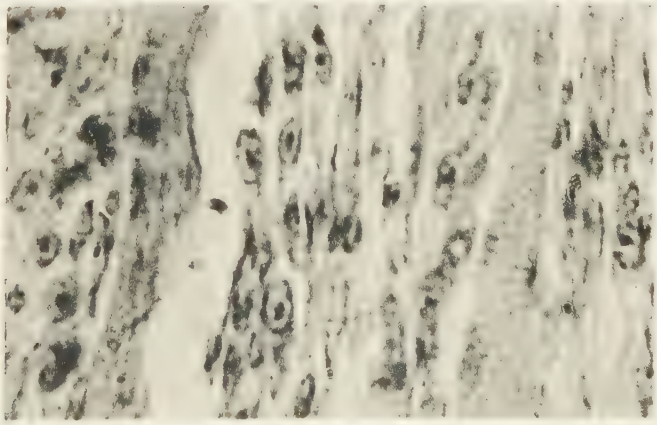

FIG. 7.

FUNGUS ASSOCIATED WITH A GRANULOMA IN A TURKISH FISH, APHANIUS CHANTREI GAILLARD.

5

Deep-sea Fishes of the Bermuda Oceanographic Expeditions. Families Cetomimidae and Rondeletiidae

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(Plate I; Text-figures 1-4)

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INTRODUCTION

IN connection with the author's systematic and morphological studies on the order Iniomi, Dr. William Beebe and Mr. John Tee-Van kindly made available the strange whale-fishes of the families Cetomimidae and Rondeletiidae obtained by the Bermuda Oceanographic Expeditions of the New York Zoological Society. While this collection comprises only six species and 16 specimens of the family Cetomimidae, it is the largest collection yet studied of one of the rarest families of deep-sea fishes. Apparently only 14 specimens and seven species have previously been recorded in the literature. Of the monotypic family Rondeletiidae, 14 examples have been mentioned in the literature. The Bermuda Expeditions add two more to this number.

The Bermuda material includes all previously known genera of both families and provides the second records and second known specimens of *Cetomimus gillii* Goode & Bean and of *Gyrinomimus simplex* Parr; the third record of *Rondeletia bicolor* Goode & Bean; the fourth record of *Ditropichthys storeri* (Goode & Bean); the fifth record for *Cetostoma regani* Zugmayer; and two new species of the genus *Cetomimus* (*C. craneae and C. teevani*). The most important results of the present investigation are the discovery for the first time of bioluminescent organs in most species of the family Cetomimidae and a unique development of the optic nerve in *Ditropichthys storeri*. In this form the eye is absent and the optic nerve passes to the surface and branches in the region where the eye should be. Also described is a new subgenus, *Psapharocetus*, of the genus *Cetomimus*, for the unique *C. kerdops* Parr. The Bermuda material has been deposited in the fish collection of Stanford University and a series has been retained by the New York Zoological Society.[1]

Practically the entire published work on the families Cetomimidae and Rondeletiidae has been done by three authors. Goode & Bean (1895) discovered both families and described two species of *Cetomimus* and one of *Rondeletia*. The other important reviews of the families are by Parr, in a series of six papers which appeared between 1928 and 1946. His main systematic review (1934) recognized four genera of Cetomimidae, two of which he described as new, and five species, two of which were new. Myers (1946) and Parr (1946b) have an interesting exchange of arguments on the relation-

[1] It is of interest to note that the remaining unworked deep-sea fishes collected by the Bermuda Oceanographic Expeditions have recently been transferred to Stanford University and are now deposited at that institution. The work on this report was done in the Natural History Museum of Stanford University.

ships of the families Cetomimidae, Rondeletiidae and Barbourisiidae. The only osteological studies of the families Cetomimidae and Rondeletiidae are by Parr (1929), describing the osteology of *Cetostoma regani* and *Rondeletia bicolor*. The single other anatomical study is by Brauer (1908) on the histology of the eye of *"Cetomimus gillii"* (identification doubtful). The history of these families can be obtained from Parr's 1928 and 1934 papers.

While considerably more research has been completed on the families Cetomimidae and Rondeletiidae than is included here, it has been deemed advisable to publish at this time only a relatively brief record of the Bermuda material and to save the remainder of the results for a general monographic review to be published in the Carlsberg Foundation reports. Dr. Å. Vedel Tåning of the Carlsberg Foundation has sent me the important world-wide collections made by the "Dana," and Dr. Carl L. Hubbs of the Scripps Institution of Oceanography is lending material obtained in the northeastern Pacific.

For data in regard to nets, localities, depths, etc., concerning the capture of cetomimids and rondeletiids treated in this report, the reader may refer to the articles by Dr. Beebe in *Zoologica* (1931a, 1931b, 1932, 1936). The numbers before the net data are the catalogue numbers of the New York Zoological Society Collection. Part of the cetomimid and rondeletiid material was listed by Beebe (1937).

Acknowledgements

To the New York Zoological Society, Dr. William Beebe and Mr. John Tee-Van, I am much indebted for the opportunity to examine the remarkable Bermuda material and for their enthusiastic cooperation during the preparation of this report. In addition they kindly supplied all field data and illustrations previously prepared. Also I wish particularly to thank Dr. Daniel Merriman and the Bingham Oceanographic Collection for the loan of the types of *Cetomimus kerdops* Parr, *Gyrinomimus myersi* Parr and *G. simplex* Parr; this allowed the study of all known species except *Cetomimus picklei* (Gilchrist) while preparing this report. Dr. Tåning and the Carlsberg Foundation have been most gracious in providing their extensive material of whale-fishes. Dr. George S. Myers aided considerably by intervening on my behalf to borrow the Bingham Oceanographic Collection types and to examine the collections of cetomimids and rondeletiids of the Carlsberg Foundation, and by helping in many other ways. The figures of *Cetomimus teevani* and *C. craneae* were ably prepared by Miss Florence Sprague. The morphological drawings are by the author.

Systematic Position of the Cetomimidae, Barbourisiidae and Rondeletiidae

The family Cetomimidae is a very little known group of deep-sea fishes, members of which have seldom been taken, only a few authors being able to examine specimens. The relationships of the group have been little understood, but it was placed in the order Iniomi by Goode & Bean (1895) and has remained there ever since. Jordan (1923) recognized the Cetomimidae and Rondeletiidae in a distinct suborder (Cetunculi). In general form and a great number of characters the Cetomimidae are most similar to the families Rondeletiidae and Barbourisiidae, and there are many reasons for considering these families to be naturally related. In fact, Myers (1946) goes so far as to place the Barbourisiidae as a subfamily of the Cetomimidae. The situation is paradoxical, however, for the Rondeletiidae are currently placed in the order Berycomorphi and the other two families in the order Iniomi. The rondeletiids used to be recognized as iniomous fishes, but Parr (1929) transferred them to the order Berycomorphi on the basis of osteological characters.

I am not yet prepared to enter wholeheartedly the argument on the systematic position of either the Cetomimidae or the Rondeletiidae, because I have not yet done enough morphological investigation, but perhaps some preliminary comments are in order. Parr's statement (1929, p. 38) that "an examination of *Rondeletia bicolor* Goode and Bean 1895a revealed this species to be a typical representative of the order Xenoberyces introduced by Regan 1911" does not seem justified at this time, nor does his statement "one may . . . also call attention to such a great number of other osteological characters in which *Rondeletia* shows a perfect concordance with the true Berycomorphi . . ." Actually very little has yet been published on the osteology of the group Xenoberyces so that a comparison could apparently be only very limited. Also *Rondeletia* does not seem to show such a perfect agreement with the order Berycomorphi as Parr concludes, for it possesses a great number of structural peculiarities unknown in any other group of fishes. In fact, there is no berycomorph that looks like a rondeletiid, so far as general appearance goes. While Parr may be perfectly right in placing the Rondeletiidae in the group Xenoberyces of the order Berycomorphi, considerably more knowledge is needed of this order before such statements can be fully justified.

One of the questions which comes to mind is that, despite the similarity in general form, and the placing of these families together in pre-

vious classifications, it remains unclear why Parr did not compare the osteology of *Rondeletia* with that of the cetomimid (*Cetostoma regani*) he examined. A possible answer became apparent while examining the cetomimids collected by the Carlsberg Foundation. This material contains some fine large *Cetostoma regani* from many widely separated regions, and it was clearly evident that the osteology of this form is probably the most aberrant in the family, and would be the most difficult from which to trace relationships.

One of the most interesting recent finds of new deep-sea fishes is Parr's (1945) discovery of *Barbourisia rufa,* which he placed in a distinct family of the order Iniomi and compared to the Cetomimidae. Myers (1946) immediately disputed Parr's recognition of the Barbourisiidae and suggested that the genus should be recognized as a subfamily of the Cetomimidae. Parr (1946b) then published a rebuttal to Myers' arguments, and continues to recognize the family Barbourisiidae. Briefly, the main points of their argument are as follows. Parr (1946b, p. 262) separated these two families primarily on the basis of three characters: "*Barbourisia* differs from all cetomimids, 1) by the presence of normal pelvic fins as compared with their complete absence; 2) by a densely spinulose skin as compared with a completely smooth and scaleless skin; 3) by a red color in life and complete absence of melanic elements in the color of the skin, as compared with a melanic pigmentation." Myers (1946) minimizes the importance of these differences, particularly in regard to separating families by the presence or absence of pelvic fins.

What is more revealing is to compare the Barbourisiidae to the Rondeletiidae, which neither Parr nor Myers did. Both groups have almost exactly the same general appearance except that the eye is larger in the latter; the pelvic fins are present in the same position in both groups, but are absent in the Cetomimidae. The distribution and formation of the head pores are the same, differing quite strikingly from the type of pore structure of the cetomimids. There are four gills and a moderate slit behind the fourth in both. The gillrakers are long and slender in both, while they are club-shaped tubercles or flat granular plates in the cetomimids. There are no teeth on the palatines in both, while teeth are always present on the palate in the Cetomimidae. *Barbourisia* differs from both the Cetomimidae and the Rondeletiidae, taken together, in only one significant character: the densely spinulose skin. In regard to Parr's character concerning the red color in life, it is now clear that all three families are red in life. Also, a species of *Gyrinomimus* from the Indo-Pacific lacks most of the melanic pigmentation normally characteristic of the Cetomimidae and is probably quite similar to *Barbourisia* in this respect.

The significance of this comparison between the Rondeletiidae and Barbourisiidae is that, on the basis of Parr's figure and description of *Barbourisia,* the two groups are closely related and separated by relatively few characters. Thus it now appears to be a question of whether this genus warrants separation from the Rondeletiidae, and *not* from the Cetomimidae. Carrying this idea farther—because *Barbourisia* shows several revealing intermediate characters in regard to lateral-line, size of eye, and palate dentition—future investigation might show that all three families should be considered as one. Such a possibility also points out the doubtful propriety of placing these families in separate orders. This is further complicated by the fact that neither family closely resembles any other members of either of the two orders (Iniomi, and Berycomorphi) in which they have been placed.

There is some reason to suspect relationships to the order Lyomeri. It is of significance that the type of luminous tissue found in the Cetomimidae is apparently similar to that found in only one other family of fishes—the Saccopharyngidae of the order Lyomeri. *Saccopharynx harrisoni* Beebe (1932b, p. 64) possesses a unique luminous caudal organ that appears from the illustration to be structurally similar to the cavernous luminous tissue around the dorsal and anal fin of the Cetomimidae. There are other superficial similarities, too. The size of the gape is approximately the same in the whale-fishes and this genus. The texture and structure of the skin seems to be the same. The granular dentition is the same in both groups. These families should be compared further.

Despite a lack of knowledge of their systematic position, the Cetomimidae, Barbourisiidae and Rondeletiidae are so similar as to suggest that they form a natural group widely distinct from all other families of fishes, and deserve at least subordinal designation, no matter where placed in the classification of fishes. Jordan (1923, p. 156) recognized them in the suborder Cetunculi of the Iniomi, and the name would be Cetomimina, using the subordinal terminology of Stenzel (1950, p. 94) that was sanctioned by the Committee on Fish Classification of the American Society of Ichthyologists and Herpetologists (see Committee on Fish Classification, 1950, and Schultz, 1951).

Family Cetomimidae

The Cetomimidae comprise at the present time four genera and nine species from the Atlantic and Indian Oceans. The Indian material is inadequately known from collections of the Deutschen Tiefsee-Expedition of the "Valdivia," reported by Brauer (1906), and of the John Murray Expedition. Following is the classification of the family as presently understood.

Subfamily Ditropichthyinae Parr (1934)
- Genus *Ditropichthys* Parr (1934)
  - *Ditropichthys storeri* (Goode & Bean, 1895)

Subfamily Cetomiminae Goode & Bean (1895)
- Genus *Cetomimus* Goode & Bean (1895)
  - *Cetomimus gillii* Goode & Bean (1895)
  - ***Cetomimus teevani,*** new species
  - ***Cetomimus craneae,*** new species
  - *Cetomimus picklei* (Gilchrist, 1922)
  - *Cetomimus kerdops* Parr (1934)
- Genus *Cetostoma* Zugmayer (1914)
  - *Cetostoma regani* Zugmayer (1914)
- Genus *Gyrinomimus* Parr (1934)
  - *Gyrinomimus myersi* Parr (1934)
  - *Gyrinomimus simplex* Parr (1946)

Dr. Carl L. Hubbs has obtained large examples of the genera *Cetomimus* and *Gyrinomimus* from the Pacific, but no specific determinations have yet been made. Most of the Carlsberg Foundation's material is from the Indo-Pacific and the group is now known to be circumtropical in distribution at great depths.

Diagnosis.—Body moderately short, somewhat compressed, scaleless. Head large, also scaleless. Mouth enormous, generally extending to or moderately behind a vertical from posterior end of cranium. Eyes very small, rudimentary or absent, situated distinctly nearer to upper jaw than to profile of top of head, in middle third of the distance between tip of snout and posterior tip of upper jaw. Teeth granular or cardiform; present on jaws, vomer and palatines; teeth in numerous rows on both jaws. Similar teeth on fused copula and upper pharyngeals. Gillrakers club-shaped or reduced to flat bony plates covered with granular teeth. Gill openings large. Gill membrane free from isthmus. Gills three or four. Dorsal and anal fins far back on body, opposite each other, with a similar number of rays. Adipose and pelvic fins absent. Pectoral fins short, placed rather low. Caudal fin short, moderately forked, truncate, or gently rounded. Lateral-line and lateral-line openings on head and body usually very large. Lateral-line on body a broad hollow tube pierced by large pores. Cavernous, intricately ridged, luminous organs often present around the anus and dorsal and anal fin bases. Luminosity presumed to be red. No photophores present. Body and head covered by a smooth, loose, dark skin. General color when alive brown or orange with brilliant orange or red jaws and fins.

Genus Ditropichthys Parr

The genus *Ditropichthys* is superficially characterized by (1) the posterior tips of the lower jaw situated approximately midway between tip of snout and opercular margin, (2) eyes absent, optic nerve extending out to opaque cornea, (3) granular teeth on the jaws and gillrakers, (4) copula (lingual bone) small, short, the sides parallel and the ends rounded, (5) the presence of spinous, club-shaped gillrakers, (6) four gills, (7) the presence of cavernous luminous tissue only in a small area at the anterior margin of the anus, (8) less than 20 rays in either the dorsal or anal fin, (9) a pair of thin dermal ridges along the ventral edge of the abdomen and a scalloped fold on each side of the anal fin base. The genus *Ditropichthys* presently includes only one species, *D. storeri* (Goode & Bean).

Ditropichthys storeri (Goode & Bean)

Specimens taken by the Bermuda Oceanographic Expeditions.—Two specimens 45.7 and 94.0 mm. in standard length; original standard lengths taken in the field before shrinkage 50 and 103 mm. respectively; from a cylinder of water eight miles in diameter (five to thirteen miles south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W. Long.

No. 18,531; net 882; 700 F.; Sept. 13, 1930; 45.7 mm.

No. 22,030; net 1148; 700 F.; Aug. 7, 1931; 94 mm.

Specimens previously recorded.—Three specimens from the Atlantic and Indian Oceans. For synonymy and discussion see Parr (1928, p. 177; 1934, p. 22) and Norman (1939, p. 32). The specimens Parr and Murray & Hjort (1912, pp. 613, 681, fig. 497) record and figure do not appear to be this species.

Description of Bermuda material.—These specimens agree well with the original description, but the smaller example is dried out. Of particular interest is the discovery that there is no eye in this form. Instead, the optic nerve appears to extend out to the opaque cornea and branch in the region where the eye should be. The implication is that the optic nerve is light sensitive. I know of no similar condition in vertebrates and plan to investigate in greater

detail. The cavernous luminous tissue is little developed, and is confined to a small half-moon shaped area bordering the anterior margin of the anus.

Field color notes prepared by Beebe.—No. 18,531, *net* 882, 45.7 *mm. in standard length.* The entire fish is a solid rich dark sepia brown.

No. 22,030, *net* 1148, 94.0 *mm. in standard length.* Interior of mouth and gills Carnelian Red[2]. Skin blackish brown. The dorsal and anal bases, and the mid-dorsal line from behind the fin almost to the caudal fin base pigmented with the same shade of red as the mouth. The bases of the caudal and pectoral fins are faintly tinged with a somewhat lighter shade of red. Finrays Raw Umber.

Genus Cetomimus Goode & Bean

The genus *Cetomimus* is superficially characterized by (1) the posterior tips of the lower jaw reaching or almost reaching the opercular opening, (2) the presence of relatively well developed eyes, (3) granular teeth on the jaws and gillrakers, (4) copula (lingual bone) fairly broad, slightly indented laterally or dumb-bell shaped, (5) the reduction of the gillrakers to flat bony plates, (6) three gills, (7) usually the presence of cavernous luminous tissue around the anus, along each side of the first anal fin rays and often around the dorsal fin origin, (8) less than 20 rays in either the dorsal or anal fin, (9) the absence of ridges on the belly or folds along each side of the anal fin. The genus *Cetomimus* presently includes five species, of which *C. kerdops* Parr and *C. picklei* (Gilchrist) are not included in the Bermuda material. The latter species was not available for study. Since it was discovered to belong in the genus *Cetomimus* subsequent to Parr's review (1934), the original description by Gilchrist (1922) and redescription by Smith (1935) should be consulted. Generic type of *Cetomimus* by subsequent designation *Cetomimus gillii* Goode & Bean.

The five species of *Cetomimus* clearly fall into two subgenera, because *C. kerdops* is so strikingly different from the other species in many characters. In addition the other three species examined, *C. gillii, C. teevani* and *C. craneae,* are closely related to each other, forming a distinct group of their own. It appears from the available descriptions that *C. picklei* belongs with the latter group. Many of the differences of *C. kerdops* from the other species are presented in the relationships of *C. craneae* and *C. teevani,* and in the key to the species of *Cetomimus.*

[2] The colors that were identified by comparison to the plates in Ridgway (1912) are capitalized.

Subgenus Cetomimus *Goode & Bean.*—This group contains four species: *C. gillii, C. craneae, C. teevani* and *C. picklei.* Subgeneric type *Cetomimus gillii* Good & Bean. Diagnosis: Head moderately compressed or depressed, considerably wider than body. Posterior tips of lower jaw well separated, not extending posterior to opercular border. Eyes very small, but fully formed. Outline of upper jaw straight, slightly convex or slightly concave. Lateral-line pores 23 or less. Each jaw with five or more longitudinal rows of teeth.

Subgenus Psapharocetus, *new.*—This group contains only one species, and therefore the subgeneric type is *Cetomimus kerdops* Parr. Diagnosis: Head strongly compressed, as wide as body. Posterior tips of lower jaw touching, extending posterior to opercular border. Eye comparatively the largest in the family except for the genus *Cetostoma;* eye fully formed. Outline of upper jaw sigmoid. Lateral-line pores on body 25. Each jaw with three irregular longitudinal rows of teeth. *Psapharo* (delicate); *cetus* (whale).

Key to the Species of the Genus *Cetomimus*

1a. Posterior tips of lower jaw widely separated; head rounded when viewed dorsally; head distinctly broader than body. (Subgenus *Cetomimus* Goode & Bean).

2a. Approximately 10 large pores in the lateral-line between gill opening and caudal fin base. . . *Cetomimus picklei* (Gilchrist)

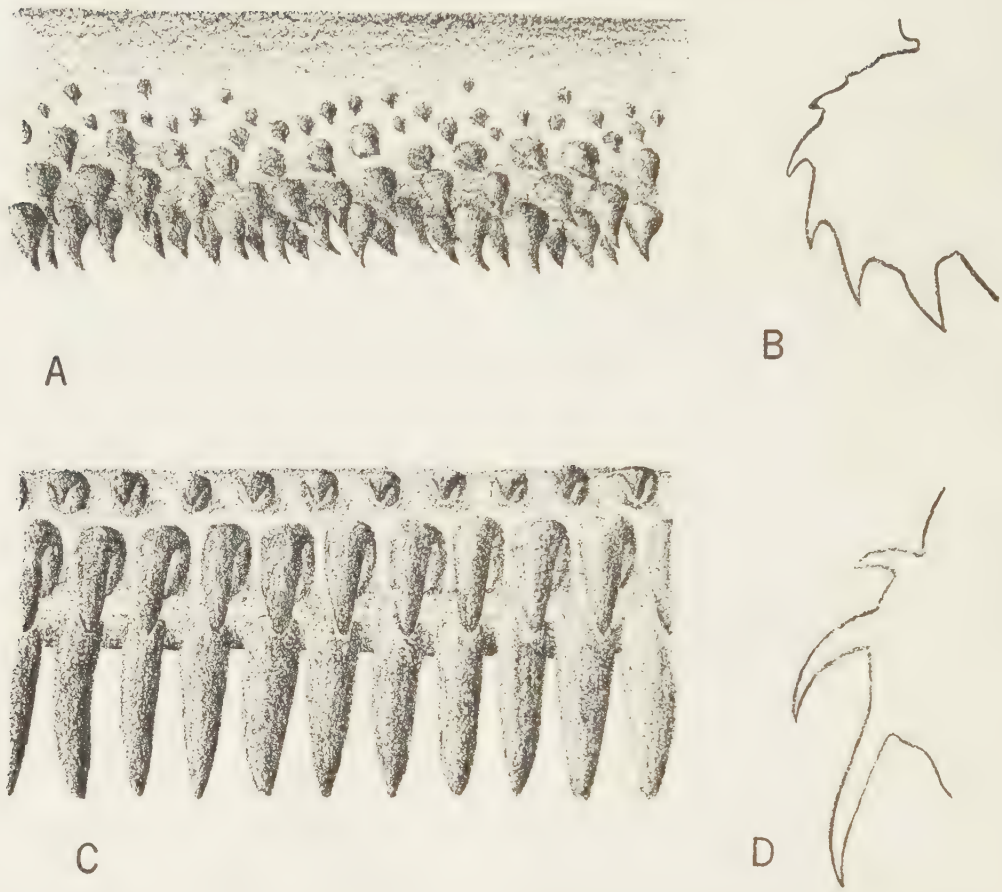
2b. Seventeen or more large pores in lateral-line between gill opening and caudal fin base.

3a. Posterior lateral-line pores without distinct lappets; pectoral fin rays approximately 16; no cavernous luminous tissue around dorsal fin origin. . . . . *Cetomimus gillii* Goode & Bean

3b. Posterior lateral-line pores with large lappets; pectoral fin rays 20-23; cavernous luminous tissue present around dorsal fin origin.

4a. Outline of upper jaw straight posteriorly, slightly convex anteriorly; cavernous dorsal luminous tissue confined to a tiny circular patch around the base of the first dorsal ray; posterior lateral-line pores small, less than half the width of the lateral-line tube, their lappets twice the diameter of the pores. . . . . *Cetomimus teevani,* new species

4b. Outline of upper jaw distinctly curved (concave); dorsal luminous



TEXT-FIG. 1. Main types of premaxillary dentition of whale-fishes. A, side view, and B, cross section, of premaxillary of *Cetomimus gillii* Goode & Bean, NYZS no. 22,677, illustrating the granular dentition characteristic of *Rondeletia*, of all known cetomimids except the genus *Gyrinomimus*, and presumably of *Bourbourisia*. C, side view, and D, cross section, of premaxillary of *Gyrinomimus simplex* Parr, NYZS no. 17,198, illustrating the unique dentition among whale-fishes of the genus *Gyrinomimus*. Since the more primitive cetomimids have the granular teeth, it is likely that the dentition of *Gyrinomimus* is a specialization from an original granular condition.

tissue extensively developed on each side along the base of the first four dorsal rays; posterior lateral-line pores large, equal to the width of the lateral-line tube, their lappets less than the diameter of the pores. . . . . *Cetomimus craneae*, new species

1b. Posterior tips of lower jaw meeting posteriorly; head sharply pointed when viewed dorsally; head as broad as body. (Subgenus *Psapharocetus*, new) . . . . . *Cetomimus kerdops* Parr

CETOMIMUS GILLII Goode & Bean

Text-figs. 1 & 2

Specimens taken by the Bermuda Oceanographic Expeditions.—Eight specimens 34.8 to 59.8 mm. in standard length; August 9, 1929, to August 21, 1931, at 700 to 1,000 fathoms; from a cylinder of water eight miles in diameter (five to thirteen miles south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W. Long.

No. 12,138; net 359; 1,000 F.; Aug. 9, 1929; 37.4 mm.

No. 13,136; net 428; 1,000 F.; Sept. 5, 1929; 38.2 mm.

No. 13,473; net 467; 900 F.; Sept. 12, 1929; 47.7 mm.

No. 17,197; net 780; 900 F.; July 5, 1930; 45.4 mm.

TEXT-FIG. 2. Spongy cavernous luminous tissue around the anus and anterior rays of the anal fin of *Cetomimus gillii* Goode & Bean. Side view facing left of NYZS no. 22,677. This figure is typical of the kind of luminous tissue found around the dorsal and anal fin origins of most cetomimids, although it is often not so well developed. It is believed that luminosity is accomplished by the exudation of a red substance, forming a luminous mucus layer over large portions of the head and body. The luminous tissue is most persistently developed around the anus and first anal fin rays, since it is seldom absent from this region.

No. 18,105; net 862; 800 F.; Sept. 8, 1930; 42.8 mm.

No. 18,628; net 892; 800 F.; Sept. 15, 1930; 59.8 mm.

No. 22,677; net 1203; 900 F.; Aug. 19, 1931; 51.6 mm.

No. 22,778; net 1216; 1,000 F.; Aug. 21, 1931; 34.8 mm.

Specimens previously recorded. — Definitely one specimen from the Atlantic and doubtfully a second from the Indian Ocean. For synonymy and discussion see Parr (1928, p. 176; 1934, p. 24).

Description of Bermuda material. — These specimens agree well with the original description, but as few essential characters were considered in that account, little is actually known of this species. The fact that the present material has approximately 16 pectoral rays, significantly agreeing with the original description in this respect, leads me to believe that this determination is correct. Cavernous luminous tissue is extensively developed around the anus and on each side of the bases of the first five anal rays; completely absent dorsally. Standard lengths were taken by Beebe in the field on two specimens. No. 18,628 was 65 mm. and no. 22,677 was 52 mm.

Field color notes by Beebe.—No. 22,677, *net* 1203, 52 *mm. in standard length.* General color blackish brown with a delicate outer membranous skin of bright Orange Chrome. The orange is especially evident on the ventral region. Inside of mouth Violet-Gray. Buccal valves bright Orange Chrome.

CETOMIMUS TEEVANI, new species

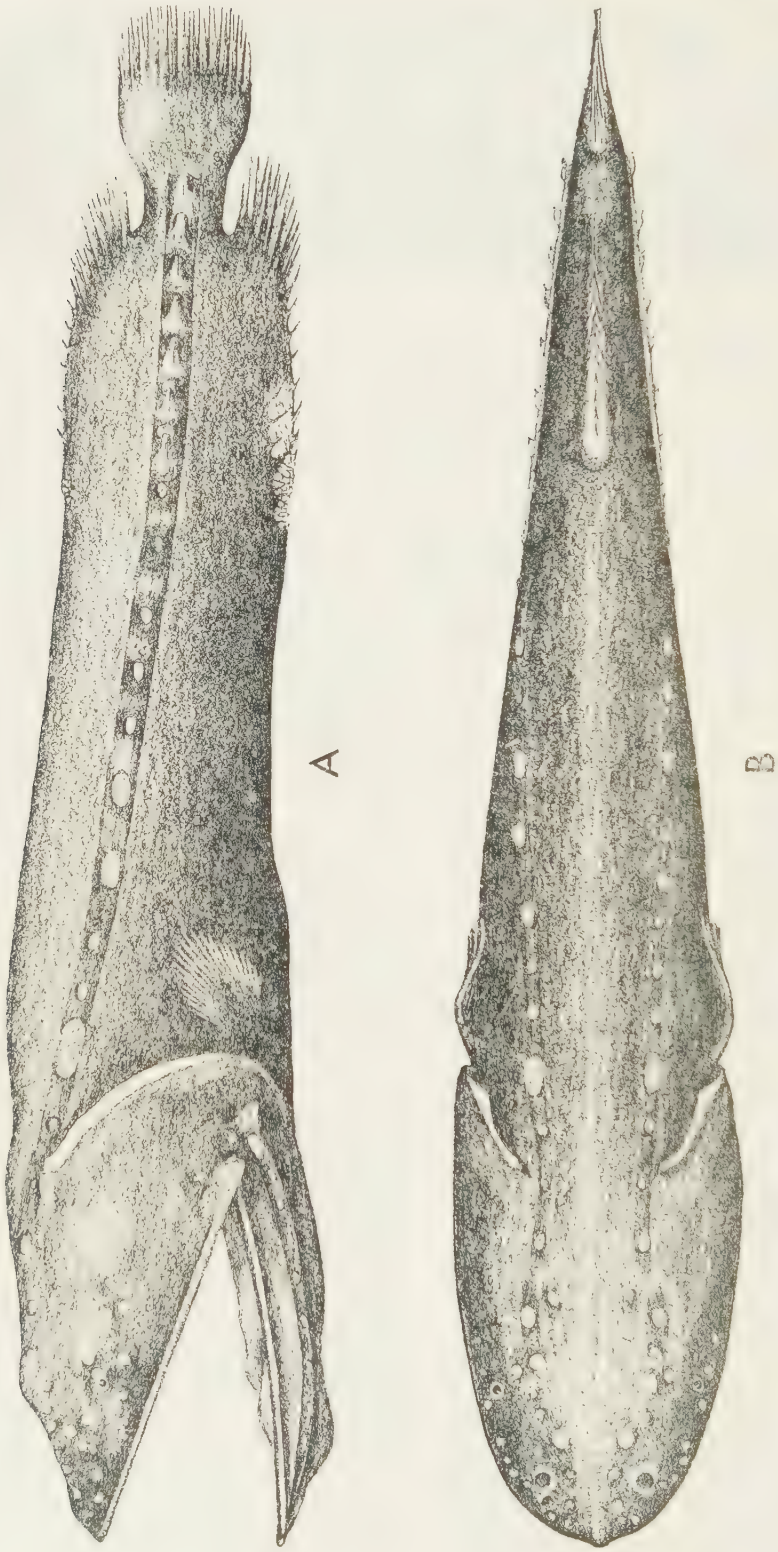
Text-fig. 3

Specimens taken by the Bermuda Oceanographic Expeditions.—Holotype 98.5 mm. in standard length; original standard length taken in field before shrinkage 105 mm.; original number 19,519; Stanford University number 17101; net 961; 700 fathoms; September 29, 1930; from a cylinder of water eight miles in diameter (five to thirteen miles south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W. Long.

Description of Bermuda material.—The only known specimen of this species is in excellent condition and well preserved. Even most of the fin rays are still complete.

Body oval in cross section immediately behind head. Greatest depth in region of pectoral fins. Caudal peduncle as long as deep. Anus immediately before anal fin; anus surrounded by extensive cavernous luminous tissue.

Head large, slightly compressed; head width slightly less than greatest head depth. Profile of snout interrupted by moderate bony projections before and above eye. Nostrils not easily distinguished, appearing exactly the same as large head pores. Nostrils without raised rims, close to upper jaw, nearer to tip of snout than to eye. Anterior nostril round, its diameter slightly less than that of the eye. Posterior nostril crescent shaped, twice as large as other nostril, close to but obliquely superior to anterior nostril. Nasal organ oblong, situated in center of anterior nostril, slightly ridged, without development of olfactory laminae. Internasal area equal to di-



TEXT-FIG. 3. **A**, Side view of holotype of *Cetomimus teevani*, new species. **B**, Top view of holotype of *Cetominus teevani*, new species.

ameter of anterior nostril. A line between eye and tip of snout touches lower border of anterior nostril. Eye very small, slightly nearer upper jaw than profile of head. Interorbital very broad, strongly convex, with a lateral and a median projection. Central part of occiput moderately rounded. Mouth enormous, moderately oblique. Dentigerous margin of upper jaw straight posteriorly, slightly convex anteriorly; that of lower jaw slightly concave. Rictus approximately 3.5 eye diameters before posterior tip of premaxillary. Jaws extend posteriorly almost to opercular margin. Mandible with a short lateral process behind tip of upper jaw and the tip of the angular produced into a short blunt spine. Distance between ricti about 2.2 into upper jaw length. Teeth on jaws granular, in many series on both jaws. The individual teeth are tiny, always pointed, and either conical or incisiform. Dentigerous edge of jaws rounded in cross section and teeth extending from outer to inner face of both jaws. Teeth in upper jaw in five (rarely six) irregular series along entire length of premaxillary. Teeth in lower jaw similar to those in upper, with approximately 120 teeth in the middle series along the mandible, extending posteriorly well beyond angle of gape. Teeth on vomer and palatines similar to those on jaws. Teeth on vomer incisiform, arranged in a circular dome-shaped patch; posteriorly they are in concentric rings; approximately 10 teeth in width and 11 teeth in length across center. Palatine series divided into two patches on each side. The teeth in the anterior section are arranged in about five concentric series; there are about 40 teeth in the longest row. The posterior tip of the anterior patch is slightly over two eye diameters before a vertical from eye. Posterior palatine dentition in a long narrow patch, extending far posterior to rictus; approximately 95 teeth in a median longitudinal series; generally five (sometimes six) series of teeth in width. Teeth on copula in a dumb-bell shaped patch with moderately pointed ends. Length of copular patch about 1.8 in snout length; with 34 rows of irregular teeth along its length; at widest point 14 series of teeth; width of copula one sixth its length. Anteriorly and posteriorly the teeth are formed in distinct wedge-shaped rows somewhat separated from the other copular teeth. The individual teeth on the copula are similar to those on the jaws. Three gill arches present, no slit behind the last. Holobranchs well developed, their length approximately twice the width of the bony gill arch. Gill-teeth granular, similar to those on jaws but smaller. Teeth on hypobranchial of first arch in a long club-shaped patch with five series of teeth at greatest width and 35 series of teeth in the central row along its length. Teeth on ceratobranchial of first arch in a single long patch with 95 teeth in a longitudinal row and five (rarely six) across. Teeth above angle on epibranchial of first arch in two patches. Near angle there is a tiny circular patch of 15 teeth; other patch long and thin, with about 40 teeth in a row along length and four teeth in width. Pharyngobranchial teeth in two elongate dome-shaped patches on each side. Individual teeth similar to those on jaws. Posterior pharyngeal patch long; 30 teeth in length, nine teeth in width. Anterior patch 24 teeth in length and 10 teeth in width.

Lateral-line a broad tube, pierced by 19 pores on body from upper edge of gill opening to base of caudal fin, the last seven pores with well developed flaps on their anterior margins; posterior pores small, much narrower than lateral-line tube; posterior flaps as long as or longer than pores. Lateral-line membrane between pores generally has one or two median mucus-tubes anteriorly and two mucus-tubes (one above the other) posteriorly. Longitudinal keel on membranes between pores only slightly developed. There are eight or nine scattered mucus-tubes on the caudal fin behind the last pore. A few scattered mucus-tubes present on back near head. Numerous large pores and a few mucus-tubes scattered over head. No crescent shaped rows of mucus-tubes above eyes. Skin loose and flabby over head and body; skin smooth, completely lacking scales or spicules. Dorsal cavernous luminous tissue confined to a small patch around the base of the first dorsal ray. Anal luminous tissue moderately well developed around anus and on each side of the bases of the first four anal rays. Otherwise no luminous organs noted.

Dorsal and anal fins far back on body. Dorsal fin origin exactly opposite anal fin origin. Dorsal fin with seven short simple rays followed by eight branched rays and one simple ray. Last two rays separate at base and counted individually. End of dorsal base exactly opposite end of anal base, measured from where the last ray contacts the profile of the body. Posterior rays of dorsal and anal fins much longer than anterior rays. Anal fin with seven short simple rays followed by eight divided rays and two simple rays. Last rays separate at base and counted individually. Pectoral fin short, low, directed obliquely upward, outline evenly rounded; pectoral rays 20 on each side, counted by dissecting the base and staining with alizarin red S. Pelvic fins absent. Caudal fin short, truncate; principal caudal rays 7 + 8.

Coloration.—Uniform solid dark brown in

alcohol. Tips of fins light. Interior of mouth lightly pigmented with brown. Buccal valves dark brown. Inside of operculum more lightly pigmented than interior of mouth. (There are no notes on life-colors accompanying this specimen).

Measurements in percent. of standard length.—Body depth measured at a vertical from region of pectoral fins, 21.5. Caudal peduncle length, which is the oblique distance between the end of the anal base and mid-base of caudal fin, 7.81. Least depth of caudal peduncle, 7.81. Head length measured from the anterior tip of the snout (upper jaw) to the most distant point of the opercular margin including membranous flaps, 37.8. Snout length measured from the tip of the snout (upper jaw) to the anterior margin of the fleshy orbit, 14.1. Upper jaw length, which is the distance between the tip of the snout and posteriormost point of the premaxillary, 30.1. Eye diameter, which is the greatest visible distance, without dissection, across the orbit, and corresponding to the diameter of the opaque cornea, 1.32. Interorbital width, which is the least fleshy width, 12.1. Greatest head width measured between the sides of the premaxillaries, 17.9. Distance between tip of snout and visible base without dissection of first dorsal fin ray, 77.6. Dorsal fin base length from origin of luminous tissue to base of last ray, 17.9. Distance between tip of snout and anus, 76.5. Length of anal fin base from anus to base of last ray, 18.0. Distance of dorsal luminous tissue behind a vertical from anus, 1.32. Length of pectoral fin measured from base of longest middle ray (found by dissection) to its tip, 9.55. Length of caudal fin from mid-base (measured from the fold when the fin is flexed from side to side) to a vertical from tip of longest ray, 12.7. Distance between origin of dorsal luminous tissue and mid-base of caudal fin, 26.7.

Relationships.—This new species belongs in the genus *Cetomimus,* agreeing completely with all characters used to distinguish the genus. In general body proportions and many characters it is intermediate between *Cetomimus gillii* and *C. craneae,* but shows only a distant relationship to *C. kerdops.* The comparisons with *C. gillii* in drawing relationships have been taken from the Bermuda specimens of this species.

Cetomimus teevani differs from the other species of the genus in (1) the formation of the dorsal cavernous luminous tissue (absent in *C. gillii,* well developed along the sides of the first dorsal rays in *C. craneae* and *C. kerdops,* confined to a small patch around the first dorsal ray in *C. teevani*); and (2) the size of the lateral-line pores (in the other species the body pores are the width of the lateral-line, in *C. teevani* most of the posterior pores are much smaller than the lateral-line width). This new species differs from *C. kerdops* and *C. gillii* but agrees with *C. craneae* in the possession of well developed lappets on the posterior lateral-line pores.

Cetomimus teevani further differs from *C. gillii* in the following characters: (1) pectoral rays 20 in the former, 16 in the latter; (2) lower jaw outline when viewed from below distinctly pointed versus evenly rounded; (3) pores bordering upper jaw between nostrils and eye distinctly smaller than eye versus considerably larger; (4) teeth in jaws considerably smaller and less distinct in *C. teevani,* about 160 teeth in the middle row of the premaxillary versus approximately 100.

Cetomimus teevani further differs from *C. craneae* in the following characters: (1) pectoral rays 20 versus 23; (2) head compressed versus as broad as deep, head width 17.9% of standard length as compared to 23.8%; (3) most of the lappets of the posterior lateral-line pores much longer than diameter of pores versus always less than diameter of pores; (4) region above tip of snout lacking mucus-tubes versus covered with over 50 tubes; (5) ends of dorsal and anal fin bases exactly opposite versus dorsal ending distinctly before a vertical from end of anal base.

Cetomimus teevani further differs from *C. kerdops* in the following characters: (1) posterior tips of lower jaw over half the snout length apart versus practically meeting in *C. kerdops;* (2) posterior process of lower jaw not reaching opercular border versus extending well beyond; (3) 19 lateral-line pores on body versus 25; (4) lower jaw inferior versus extending slightly before upper jaw; (5) opercular membranes at isthmus join well behind a vertical from eye versus joining below a vertical from eye.

Name.—This species is named in honor of Mr. John Tee-Van in appreciation of his important part in the Bermuda Oceanographic Expeditions.

CETOMIMUS CRANEAE, new species

Text-fig. 4

Specimens taken by the Bermuda Oceanographic Expeditions.—Holotype 82.4 mm. in standard length; original number 11,370; Stanford University number 17102; net 269; 800 fathoms; July 8, 1929; from a cylinder of water eight miles in diameter (five to thirteen miles

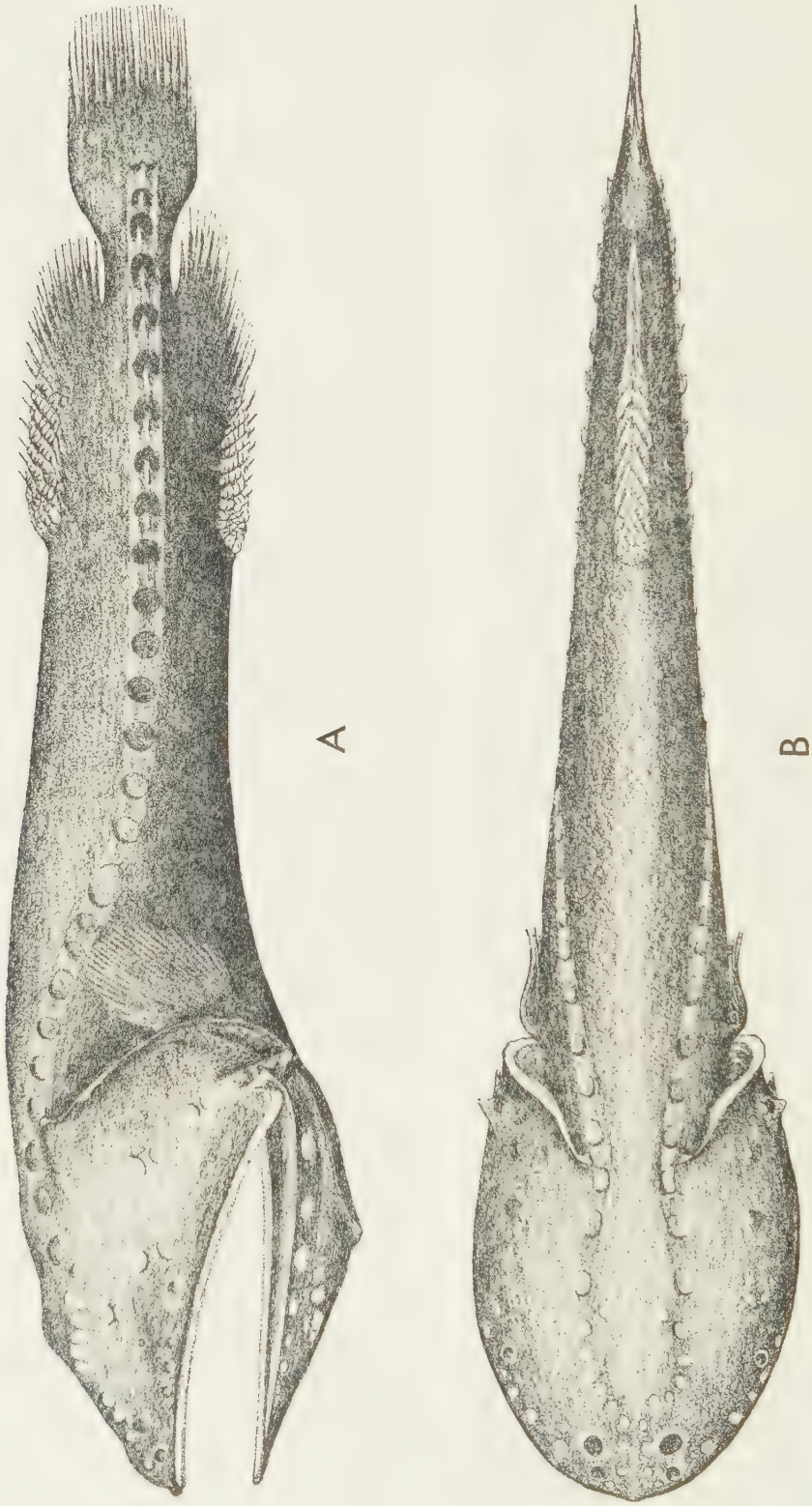
south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W. Long.

Description of Bermuda material.—The only known specimen of this species is in exceptionally fine condition and not damaged in any way. Most of the fin rays are still complete.

Body moderately oval in cross section immediately behind head. Greatest depth immediately behind head. Length of caudal peduncle slightly greater than its least depth. Anus immediately before anal fin, surrounded by extensive cavernous luminous tissue.

Head large, its width equal to its depth. Profile of snout evenly rounded onto occiput. Nostrils not easily distinguished, appearing exactly like the head pores. Nostrils round, of equal size, close to premaxillary; both large, without raised rims except that the anterior nostril has a slight swollen lobe at its anterior margin. Nasal organ tear-drop shape, without any trace of distinct olfactory laminae, situated internally between the two nostrils. Internasal membrane same size as diameter of nostrils. A line between eye and tip of snout passes through anterior nostril; posterior nostril above this line. Eye very small, much nearer upper jaw than profile of head. Interorbital very broad, strongly convex, with two median longitudinal humps. Central part of occiput flat. Mouth enormous, moderately oblique. Dentigerous margin of both jaws slightly concave. Rictus approximately four eye diameters before posterior tip of premaxillary. Jaws extend posteriorly to opercular margin. Mandible with a short lateral process behind end of upper jaw and the tip of the angular is produced into a short blunt spine. Distance between ricti about 1.3 into upper jaw length. Teeth on jaws granular, in many series on both jaws. The individual teeth are tiny and either conical with their lengths equal to their basal diameter or else incisiform with a flat outer margin. Edge of jaws rounded in cross section and teeth extending from outer to inner face of both jaws. Teeth in upper jaw in six irregular series along entire length of premaxillary; anteriorly the innermost series is separated from the remaining teeth by a narrow space. There are approximately 140 teeth in the middle row along the premaxillary. Teeth in lower jaw similar to those in upper, with approximately 120 teeth in the middle series along the mandible, extending posteriorly behind angle of gape. Teeth on vomer and palatines similar to those on jaws. Teeth on vomer incisiform, in an oval dome-shaped patch; anteriorly the teeth are in concentric rings. There are approximately 12 teeth across and 14 teeth along the length of the vomer. Palatine series divided into two patches on each side. The teeth in the anterior section are arranged in about twelve concentric series; there are about 40 teeth in longest row. The posterior tip of the anterior patch is an eye diameter anterior to a vertical from the eye. Posterior palatine patch long, fairly broad, extending well posterior to rictus; there are slightly over a hundred teeth in a longitudinal series, 10 series of teeth in width. Teeth on copula in a dumb-bell shaped patch; copula with a moderately pointed anterior end and rounded posterior margin. Length of copular patch about 1.5 in snout length, with 28 rows of irregular teeth along its length; at widest point 17 series of teeth; width of copula one-third its length. Anteriorly the copular teeth are arranged in distinct wedge-shaped rows, posteriorly these merge into a closely packed mass. The individual teeth on the copula are round at the base and incisiform at the tip. Three gill arches present, no slit behind last. Holobranchs well developed, their lengths approximately twice the width of the bony gill arch. Gill-teeth granular, similar to those on jaws but more feebly developed. Teeth on hypobranchial of first arch in a single flat club-shaped patch; six series of teeth at greatest width and 30 teeth in middle row along its length; the individual teeth are in irregular longitudinal series. Teeth on ceratobranchial of first arch in a single long bony patch of irregular outline; the teeth are in irregular patches, some in longitudinal series and others in oblique series; there are approximately 90 teeth in longitudinal series and 10 across the bone. Teeth above the angle on epibranchial of first arch in two patches; near angle there is a small crescent-shaped patch of about 10 teeth in width; other patch long and thin with about 28 teeth along its length and six teeth across its width. Pharyngobranchial teeth developed in two cone-shaped bony patches on each side; individual teeth similar to those on jaws. Posterior pharyngobranchial patch oval, 24 teeth in length, 15 teeth in width. Anterior patch 23 teeth in length and 12 teeth in width.

Lateral-line a broad tube pierced by 22 large pores on body, the last nine pores with well developed flaps on their anterior margins; lateral-line pores same size as tube, their lappets always shorter than diameter of pores. In addition, the last sections have a longitudinal keel on the membranes between the pores. Lateral-line membranes between pores generally have one median mucus-tube anteriorly and two mucus-tubes (one above the other) posteriorly. There are eight mucus tubes in groups of two on the caudal fin behind the last lateral-line pore. Scattered mucus-tubes present along mid-



TEXT-FIG. 4. **A**, Side view of holotype of *Cetomimus craneae*, new species. **B**, Top view of holotype of *Cetomimus craneae*, new species.

line of back. Lateral-line pores continued on head forward onto snout. Numerous large cavernous pores and many mucus-tubes scattered over head. No crescent-shaped rows of mucus-tubes above eyes, but a curved row is present across interorbital on top of head. Skin loose and flabby over head and body, completely lacking scales or spicules. Cavernous luminous tissue well developed around origins of dorsal and anal fins and on each side of the bases of the first four rays of these fins; also extensively formed around anus. Otherwise no luminous organs noted.

Dorsal and anal fins far back on body. Dorsal fin origin slightly anterior to anal fin origin. Dorsal and anal fin with seven short simple rays followed by nine branched and one simple ray. Last two rays separate at base and counted individually. End of dorsal base slightly in advance of anal fin base. Posterior rays of dorsal and anal fins much longer than anterior rays. Pectoral fin short, fairly low, directed obliquely upward, outline evenly rounded. Pectoral rays 23 on each side; counted by dissecting pectoral fin base. Pelvic fins absent. Caudal fin short, slightly emarginate; principal rays 6 + 8.

Coloration.—Uniform solid dark brown in alcohol. Tips of fins light. Roof of mouth lightly pigmented brown; floor of mouth darker. Buccal valves dark brown. Inside of operculum lightly pigmented brown.

Field color notes prepared by Beebe.—The fish at first was a dark brown tinged with Terra Cotta. Before being put in preservative the epidermis became loose. After a night in 3% formalin, the entire epidermis was blown away with a pipette. The fish then became a dark Seal Brown. (It is probable that the "epidermis" referred to was a coating of coagulated mucus, for the fish still possesses its epidermis).

Color notes from field drawings.—Two color illustrations were prepared of the holotype by Helen Tee-Van (B127, no. 284). One of them shows the specimen as being a solid orange over head, body and fins and must have been prepared before preservation. The other illustration is in much greater detail and corresponds to Beebe's notes. The general color is a dark brown. The jaws, fins and pores are tinged with orange, particularly the cavernous luminous tissue and vertical fins.

Measurements in percent. of standard length.—Body depth measured at a vertical from posterior tip of head, 20.9. Caudal peduncle length, which is the oblique distance between the end of the anal fin base and mid-base of caudal fin, 10.6. Least depth of caudal peduncle, 5.70. Head length measured from the anterior tip of the snout (upper jaw) to the most distant point on the opercular margin including membranous flaps, 36.7. Snout length measured from the anterior tip of the snout (upper jaw) to the anterior margin of the fleshy orbit, 12.5. Upper jaw length, which is the distance between the tip of the snout and posteriormost point of the premaxillary, 28.9. Eye diameter, which is the greatest visible distance without dissection across the orbit, .85. Interorbital width, which is the least fleshy width, 14.9. Greatest head width measured between posterior tips of lower jaw while head was freely suspended, 23.8. Distance between tip of snout and visible base without dissection of first dorsal fin ray, 76.7. Dorsal fin base length from origin of luminous tissue to base of last ray, 18.6. Distance between tip of snout and anus, 70.8. Length of anal fin base from anus to base of last ray, 18.4. Distance of dorsal luminous tissue before a vertical from the anus, 2.31. Distance between end of dorsal fin base posteriorly to a vertical from end of anal fin base, .85. Length of pectoral fin measured from base of longest middle ray (found by dissection) to its tip, 8.86. Length of caudal fin from mid-base (measured from the fold when the fin is flexed from side to side) to tip of longest ray, 10.2. Distance between origin of dorsal luminous tissue and mid-base of caudal fin, 29.4.

Relationships.—This new species clearly belongs in the genus *Cetomimus,* agreeing completely with all characters used to distinguish the genus. In general body proportions and many characters this species is most closely related to *C. teevani* and shows the closest relationships to the genus *Gyrinomimus* of any species outside that genus. The head is broad, and the outlines of the jaws distinctly concave as in *Gyrinomimus.* This new species is much more closely related to *C. gillii* than to *C. kerdops.*

Cetomimus craneae differs from the other species of the genus in (1) the more extensive development of the cavernous tissue than any other known species in the family; (2) having the head as broad as deep versus distinctly compressed in the other species of *Cetomimus;* (3) having the highest number of pectoral fin rays in the genus, 23 versus 16-20; (4) the presence of great numbers of mucus-tubes over the head and back which are only sparsely present in the other species; this condition is most closely approached by *C. gillii,* but there are considerably fewer in this form.

Cetomimus craneae further differs from *C. gillii* in the following characters: (1) outline of jaws distinctly concave versus straight in *C.*

gillii; (2) posterior lateral-line pores possessing well developed lappets versus lappets vestigial or absent; (3) dorsal cavernous luminous tissue present versus absent; (4) pores bordering upper jaw between nostrils and eye distinctly smaller than eye versus considerably larger than eye; (5) sides of copular patch strongly indented versus practically straight.

Cetomimus craneae further differs from *C. kerdops* in the following characters: (1) Posterior tips of lower jaw over three-fourths of the snout length apart versus practically meeting in *C. kerdops;* (2) opercular membranes at isthmus join well behind a vertical from eye versus joining below a vertical from eye; (3) posterior lateral-line pores possessing well developed lappets versus lappets absent; (4) sides of copular patch strongly indented versus practically straight; (5) head considerably wider than body versus as wide as body.

Further comparisons to the other species of *Cetomimus* are given in the section on relaships of *C. teevani.*

Name.—This unusual fish is named in honor of Jocelyn Crane in recognition of her work on deep-sea fishes.

Genus Cetostoma Zugmayer

The genus *Cetostoma* is superficially characterized by (1) having the posterior tips of the lower jaw extend well posterior to the opercular opening, (2) the presence of relatively completely developed eyes, (3) having granular teeth on the jaws and gillrakers, (4) having the copula (lingual bone) very narrow, long and slender, somewhat expanded at anterior tip, (5) the reduction of the gillrakers to flat bony plates, (6) having three gills, (7) the presence of a tiny area of modified cavernous luminous tissue on each side of anus, but none elsewhere, (8) having approximately 30 rays in both dorsal and anal fins, and (9) the presence of a low ventral median fold on belly from below pectoral fins to anus, but lack of folds on each side of anal fin. The genus *Cetostoma* includes a single remarkable species, *C. regani* Zugmayer, which shows many unique differences from all other genera. Its closest relationships lie with *Cetomimus kerdops.* It should be noted that this determination of genus and species is made on the basis of Parr's findings, because Zugmayer's original description is useless.

Cetostoma regani Zugmayer

Specimens taken by the Bermuda Oceanographic Expeditions.—Two specimens 41.8 and 43.7 mm. in standard length; original number 17,196; net 778 at 700 fathoms, July 5, 1930; from a cylinder of water eight miles in diameter (five to thirteen miles south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W. Long.

Specimens previously recorded.—Three specimens from the Atlantic. See Parr (1934), and Murray & Hjort (1912, pp. 613, 682, fig. 498).

Description of Bermuda material.—Both specimens are in rather poor condition, having partially dried out at one time, but there appears to be no question of their identity. The standard lengths were probably 10-15 mm. longer before preservation. Normal cavernous luminous organs are not present in this form, but there appears to be modified luminous tissue of this basic type in a small narrow ridge on each side of the anus.

Genus Gyrinomimus Parr

The genus *Gyrinomimus* is superficially characterized by (1) the posterior tips of the lower jaw reaching the opercular openings, (2) the presence of relatively well developed eyes, (3) having elongate cardiform teeth on the jaws and granular teeth on the gill arches, (4) having the copula (lingual bone) broad, shield-shaped, moderately pointed anteriorly and expanded laterally posteriorly, (5) the reduction of the gillrakers to flat bony plates, (6) having three gills, (7) the complete absence of cavernous luminous tissue, or if such is present, by having it only faintly formed around base of first dorsal ray and around anus, (8) having less than 20 rays in both the dorsal and anal fins, and (9) the absence of ridges on the belly or folds along each side of the anal fin. The genus *Gyrinomimus* includes two species of which *G. myersi* is not included in the Bermuda material. Generic type by original designation, *Gyrinomimus myersi* Parr. This genus is most closely related to *Cetomimus,* particularly through *C. craneae,* to which it shows the greatest similarities.

Gyrinomimus simplex Parr

Text-fig. 1

Specimens taken by the Bermuda Oceanographic Expeditions.—One specimen 48.3 mm. in standard length; original standard length before shrinkage 54 mm.; original number 17,198, net 732 at 900 fathoms, June 27, 1930; from a cylinder of water eight miles in diameter (five to thirteen miles south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W .Long.

Specimens previously recorded.—One specimen from the Atlantic. See Parr (1946).

Description of Bermuda material.—This specimen agrees well with the holotype. The posterior

lateral-line pores are round, completely lacking lappets. No cavernous luminous tissue.

Family Rondeletiidae

The family Rondeletiidae has been reported upon only three times. The original description (later copied by various authors) was made by Goode & Bean (1895) from a single specimen, which was placed in the order Iniomi. Parr (1928) recorded and briefly described 13 specimens, and in 1929 he considered the osteology in considerable detail, placing the family in the group Xenoberyces of the order Berycomorphi. As previously stated, Myers (1946) and Parr (1946b) have interesting arguments about the systematic position of this family. Apparently only two illustrations giving the aspect of the unique species have been prepared. The first figure appeared with the original description by Goode & Bean and has been used by several subsequent authors. The second illustration is a colored plate prepared under the direction of Dr. William Beebe that has appeared in the National Geographic Magazine (Beebe, 1931). Since this latter plate is of considerable importance in establishing the coloration of this group and is more accurate than the original figure, it has been reproduced with this paper.

The Rondeletiidae include only one genus and species, *Rondeletia bicolor* Goode & Bean.

Rondeletia bicolor Goode & Bean

Plate I

Specimens taken by the Bermuda Oceanographic Expeditions.—Two specimens 24.7 and 86.7 mm. in standard length; original standard lengths taken in field before shrinkage 25.7 and 97 mm. respectively; from a cylinder of water eight miles in diameter (five to thirteen miles south of Nonsuch Island, Bermuda), the center of which is at 32° 12′ N. Lat., 64° 36′ W. Long.

No. 13,434; net 463; 1000 F.; Sept. 11, 1929; 86.7 mm.

No. 23,339; net 1291; 600 F.; Sept. 12, 1931; 24.7 mm.

Specimens previously recorded. — Fourteen specimens from the Atlantic. See Parr (1928, p. 179; 1929, p. 39).

Description of Bermuda material.—The two Bermuda examples agree quite closely with the previous descriptions. No luminous structures are found, but it is believed that the orange areas in life are luminous. It is of particular significance that its coloration in life is very similar to that known for most members of the Cetomimidae.

Field color notes by Beebe. — The colored plate of this species has obviously been prepared from no. 13,434, but the original color notes are not available. From the color plate it can be seen that the fish is dark brown with bright reddish-orange jaws, and that the fin bases are also reddish-orange.

No. 23,339, *net* 1291, 24.7 *mm. in standard length.* General color blackish-brown. The pelvic fins are strikingly webbed with scarlet. Remainder of color notes not complete enough to be included.

Summary

The families Cetomimidae and Rondeletiidae are remarkable groups of rare luminous whale-like fishes, about two to six inches long, which have been sporadically collected in the Atlantic and Indian Oceans. The systematic position of these families has aroused some argument, but appears to be in the neighborhood of the orders Iniomi, Berycomorphi, and perhaps the Lyomeri. The families Cetomimidae, Barbourisiidae and Rondeletiidae seem to form a naturally related group with the second named group intermediate in position, but considerably closer to the Rondeletiidae.

Previous specimens of the family Cetomimidae had been placed in four genera and seven species. In the course of the oceanographic work of the Department of Tropical Research of the New York Zoological Society, during nine years' investigation within an eight-mile circle off Bermuda, sixteen cetomimids and two rondeletiids were obtained. This collection, while small in number, has added considerably to our knowledge of these excessively rare fishes. This material again shows the great value of concentrated research to find out just what part of the total bathypelagic fish fauna could be taken in a restricted area. In regard to the Cetomimidae and Rondeletiidae, all known genera were taken and all but three of the previously known species. In addition two new species of the genus *Cetomimus* were collected (*C. craneae*, *C. teevani*), these being of particular value in tracing the relationships of the genera *Cetomimus* and *Gyrinomimus*. All the Bermuda material was taken between the depths of 700 and 1,000 fathoms.

Dr. Beebe's field notes give the first life color information ever obtained on these strange fishes. These notes reveal the "orange-mouths," or "giant-mouth orange-skins" as Beebe termed them, to be usually of a solid orange or brown in life with bright orange or reddish-orange mouths and fins.

Bioluminescence has not been previously dis-

cussed in the family Cetomimidae, although these fishes are apparently luminous. Most species of this family have peculiar webbed, spongy, cavernous tissue around the anus and the first dorsal and anal fin rays; these tissues appear to represent luminous organs. This type of luminous structure appears to be similar to that found in only one other species of fish, *Saccopharynx harrisoni* Beebe, a gulper eel of the order Lyomeri. Since the cavernous tissue of the cetomimids is red or reddish-orange in life, it is presumed that the luminescence may also be of these colors. The peculiar luminous tissue of *S. harrisoni* glows scarlet, apparently showing a similarity to the cetomimids in this respect.

A remarkable discovery is the complete absence of eyes in the cetomimid, *Ditropichthys storeri*. Instead, the optic nerve extends out to a heavily pigmented area in the opaque cornea and branches near the surface of the skin. The implication is that the optic nerve is light-sensitive but further study is needed before more can be said of this condition, which is unique among vertebrates.

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EXPLANATION OF THE PLATE.

Plate I.

Adults of the rare whale-fish, *Rondeletia bicolor*, feeding on very small crustaceans. The coloration was noted before preservation, establishing that these unusual fishes are red in life to a considerable extent. (From a painting by E. Bostelmann).

DEEP-SEA FISHES OF THE BERMUDA OCEANOGRAPHIC EXPEDITIONS.
FAMILIES CETOMIMIDAE AND RONDELETIIDAE.

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